# EIFELIAN BRACHIOPODS FROM PADAUKPIN, NORTHERN SHAN STATES, BURMA

M. M. ANDERSON, A. J. BOUCOT & J. G. JOHNSON



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#### SYNOPSIS

The articulate brachiopods from the Padaukpin area include thirty-two species assigned to thirty-one genera. *Cimicinoides struvei* is proposed as a new genus and species of terebratulid brachiopods. The fauna has marked affinity with the Eifelian brachiopod fauna of western Europe and is concluded to be of Eifelian age. From a provincial point of view it is noteworthy that the Padaukpin brachiopods have stronger affinity with European Eifelian brachiopods than those of regions to the north in the U.S.S.R.

Padaukpin conodonts and foraminifera, previously undescribed, are also referred to in the discussion on the age of the brachiopod fauna.

#### I. INTRODUCTION

A LARGE collection of fossils was made between 1959 and 1961 from fossiliferous beds close to Padaukpin, some ten miles east-north-east of the administrative centre of Maymyo (Text-fig. 1a), in the Northern Shan States of Burma while one of us (M.M.A.) was Colombo Plan Visiting Professor of Geology at the University of Mandalay. This site is an historic one as the fossils have long been used locally as charms and about the middle of the last century King Mindoon Min had pits dug in the area because it was thought that the fossils indicated hidden treasure. The first geologist to visit Padaukpin was La Touche of the Geological Survey of India who several years later published a Memoir on the Geology of the Northern Shan States (1913) which is still the only authoritative work on the region, as little has been published on any aspect of the geology of this part of Burma, apart from mineral deposits of economic interest, since that date. La Touche collected a great variety of fossils which were described by Cowper Reed (1908).

Padaukpin (lat. 22° 5′ 48″, long. 96° 37′ 30″)¹ is a small village lying about a mile east-south-east of Wetwin railway station on the Mandalay Lashio railway which here

<sup>1</sup>La Touche (1913), Cowper Reed (1908 on information supplied by La Touche), and later writers quoting these works give the position of Padaukpin as lat. 22° 6′ 30″, long. 96° 44′, but more accurate surveying since that time shows that the lines of latitude and longitude on the maps which accompany La Touche's Memoir are slightly incorrect.



Fig. 1a. Outline map of Burma showing the position of Maymyo.

runs more or less parallel to the main road from Maymyo to Lashio (see Text-fig. 1b). Just before the road reaches the railway station it is joined by a motorable track which runs almost east and then south-east to a power station on the Ge-raung chaung¹ (chaung = stream). This track passes to the west and south of Padaukpin and it is along the bullock-cart tracks that lead from it to the western side of the village that the exposures described by La Touche (1913) occur. The exposures are present, however, only over a short distance of about 20 yards before the entrance

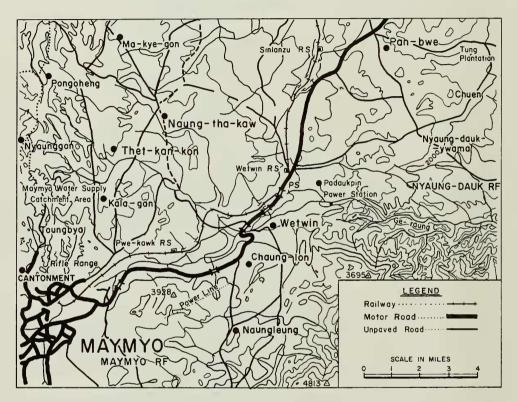


Fig. 1b. Wetwin area, east of Maymyo, with Padaukpin village lying about one mile east-south-east of Wetwin railway station.

to the village where the bullock-cart tracks lead up over a gentle rise marking the position of the limestone beds; laterally the beds can be traced for about a hundred yards. Even over this small area only a few low rounded outcrops of small size appear through the overlying clay soil which is covered with bushes and trees between the tracks, so that exposures are practically confined to the places where the wheels of the bullock-carts have cut through the clay and exposed bedrock. The beds dip gently to the east and probably only about ten feet of limestone beds are present. Fossils were difficult to extract from the hard limestone but large

<sup>&</sup>lt;sup>1</sup>Spelt Ke-laung on map accompanying La Touche's Memoir (1913).

numbers were collected from the overlying clay which has resulted from the *in situ* weathering of the limestone.

A second, previously unknown, fossil locality at the same horizon was found to occur along the strike of the limestone beds on another gentle bush and tree covered slope south of Padaukpin. A footpath runs south from the village to join the motorable track to the power station, and the locality occurs just east of the path about a quarter of a mile from the village (see Text fig.-Ic). The limestone beds are again poorly exposed but their presence is indicated by the large number of fossils which have weathered out. These were collected over an area similar in extent to the first locality. Here, however, the overlying clay is much thinner and large colonies of tabulate

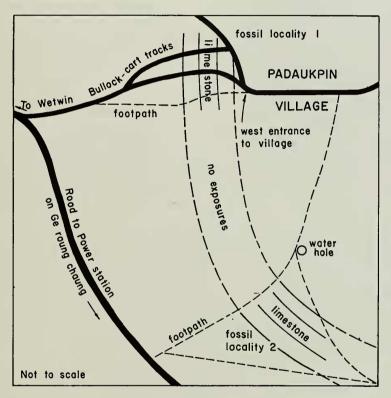


Fig. 1c. Fossil localities at Padaukpin.

corals and stromatoporoids were lying on the surface or close to it, apparently undisturbed, in their original positions of growth.

The collection of fossils from Padaukpin described by Cowper Reed (1908) included species belonging to the following invertebrate groups: corals (tetracorals and tabulates), stromatoporoids, brachiopods, crinoids, bryozoa, lamellibranchs, gastropods, cephalopods, trilobites, and annelids. In addition to these groups the new collection from the two Padaukpin localities contains conodonts, foraminifera,

ostracodes, sponges, tentaculites, blastoids, and echinoids; the conodonts were isolated by Dr. Gilbert Klapper of Pan American Petroleum Corporation, Tulsa, Oklahoma, from a relatively small sample of the limestone, and his report is given below. Dr. D. F. Toomey, also of the Pan American Petroleum Corporation, has provided information on the foraminifera extracted from the same sample (see page 117 and Toomey 1968). The Padaukpin fauna thus includes not only benthonic forms but also the remains of some of the pelagic and planktonic micro-organisms which were living in the overlying waters at the same time.

Conodonts, ostracodes, sponges, tentaculites, blastoids, and echinoids have not previously been recorded from the Devonian of Burma. Unfortunately no complete sponges or echinoids were discovered; the presence of the former is indicated by abundant loose spicules while the latter are represented by spines, which are fairly common, and, more rarely, by individual interambulacral plates. La Touche did not find any foraminifera at Padaukpin but he mentioned the presence of numerous minute foraminifera, including species of *Endothyra*, *Textularia* and possibly *Trochammina*, in an oölitic dolomite near Mongyaw (1913:191) which is also considered to be Devonian in age.

La Touche (1913) described the Padaukpin limestones as a coral reef. There is, however, no development of a reeflike structure at either locality and although corals represent an important part of the fauna they are probably matched in abundance by stromatoporoids, brachiopods, crinoids and possibly even by bryozoa so that a special emphasis on corals is misleading. The limestones were laid down as distinct beds and since they consist largely of the remains of organisms and are almost entirely of biochemical origin they can be referred to as biostromes (Cummings 1932). An account of the palaeoecology of the fossil communities within the Padaukpin biostromes will be published elsewhere.

The area between the two localities, which is partly cultivated and partly covered with thick vegetation, was carefully searched for exposures of limestone, but none were found; attempts to find the bed elsewhere in the district were equally unsuccessful. This was not for lack of outcrops in the vicinity as the bedrock is well exposed, and even though some of the outcrops are only a few yards away from the Padaukpin limestone beds, in all cases it is found to be dolomite. It seems likely, therefore, that, as was first suggested by La Touche (Cowper Reed 1908, from notes supplied by La Touche), the limestones are interbedded with the dolomite. They also appear to pass laterally into dolomite as shown by the fact that along the strike of the Padaukpin beds, a short distance south of the second locality, dolomite is present in which the outlines of fossils can be recognized, and brachiopods in particular are represented by cavities with a drusy lining of dolomite. Such cavities are rarely seen elsewhere in the dolomite beds which have a wide distribution in the Northern Shan States and generally appear to be unfossiliferous. However, these dolomites do occasionally show traces of fossils, generally indeterminate but sometimes the outlines of corals, crinoid ossicles, brachiopods, and foraminifera can be made out.

Thin sections of the fossiliferous dolomite of the Padaukpin area, and of the dolomites from elsewhere that show traces of fossils, reveal that the original shell or skeletal

material has been completely replaced by dolomite and the structure of the fossils totally destroyed. The former presence of fossils is indicated by ghost structures, by dust particles outlining the original shapes, and by differences of grain size between areas formerly occupied by fossils and the surrounding matrix. In the last case the large, but variable, size of the dolomite grains of the matrix contrasts with the small and uniform size of the grains which have replaced the fossil structures: this difference is probably attributable to selective replacement. The outlines of fossil fragments are, in general, only discernible and not readily recognizable but occasionally they can be identified; La Touche (1913:192) drew attention to the fact that foraminifera are the only organisms within the dolomite to have escaped replacement. He also described oölitic dolomite (1913:191) in which some of the oöids still show a concentric structure of alternate minutely crystalline and "dirty" bands while others are represented only by circular or oval outlines within which there is a partial or complete filling of large euhedral crystals of dolomite.

The presence of oöids, recognizable fossils and discernable but unidentifiable

The presence of oöids, recognizable fossils and discernable but unidentifiable fossils in the dolomite beds (the positive and negative relicts of Teodorovich 1958) is proof of the replacement origin of the dolomite. The dolomite beds in the Northern Shan States, with which the Padaukpin limestones are associated, have thus originated by replacement of calcium carbonate during diagenesis, and the Padaukpin limestones therefore represent a part of the sequence which escaped dolomitization. Although this dolomitization was regional in extent it must have operated selectively as apart from the Padaukpin limestones, other "patches" of limestone are known within the succession which have escaped replacement or suffered only partial dolomitization.

The limestones and dolomites of the Padaukpin area belong to the Plateau Limestone. La Touche (1913: 182) gave this name to the "limestones" because they underlie the greater part of the plateau country of the Shan States and their weathering is responsible for the distinctive scenery of these upland areas; he considered them to range from Devonian to Permian in age. The systematic survey of the geology of the Northern Shan States by La Touche and his colleagues of the Indian Geological Survey, which culminated in his Memoir (1913), was carried out during field seasons from 1899 to 1912, and it seems likely that this name was adopted before they realized that the Plateau Limestone is, in fact, almost entirely a dolomite formation. True limestones, which overlie the dolomite beds and yield a different fauna, represent only the upper part of the formation which is very much thinner than the lower part of this carbonate sequence. Therefore, when La Touche came to write his Memoir he divided the formation on a lithological and a faunal basis into a lower section to contain the dolomite beds with a Devonian fauna and an upper or Anthracolithic section for the limestones with a Permo-Carboniferous fauna.

The name Plateau Limestone is clearly inappropriate for either the formation as a whole, or for one or other of its subdivisions, because the lower is dominantly dolomitic with only subordinate limestones while the upper is not restricted to plateau country, and the true limestones are, in any case, less widespread in the Northern Shan States than the beds of dolomite. For the time being no nomenclatorial revision is attempted.

The two divisions of the Plateau Limestone were not mapped separately by La Touche (1913) because he believed that the lower passed without any stratigraphic break into the upper thus giving a Carboniferous to Permian age range for the true limestones. However, no diagnostic Carboniferous fossils have yet been found in these limestones and, in spite of its apparent conformity, Holland *et al.* (1956) and the authors regard the upper section of the Plateau Limestone as a separate formation, Permian in age.

The lower, Devonian, division of the Plateau Limestone is of considerable thickness; La Touche (1913: 186) estimated that in the valley of the Nám Tu river north of Hsipaw it was about 6,600 feet. Even this figure represents an underestimate because the top of the formation in this area was eroded before the deposition of the overlying Jurassic strata, and the lowermost beds, here resting on Silurian or Lower Devonian sandstones, are probably not the actual basal beds as there is a progressive overlap of older beds by younger beds within this formation. However, the general scarcity of fossils within the dolomite beds makes it impossible at present to determine which part of the Devonian is represented by a particular locality in the Northern Shan States with the exception of the beds in the immediate vicinity of the fossiliferous localities of Padaukpin, Wetwin, and one small area in the valley of the Kelaung chaung (= Ge-raung chaung). Although these three localities are all within a few miles of one another (see Text-fig. 1b) they appear to represent three different horizons within the Devonian. Unfortunately it has not been found possible to trace these beds laterally so that their field relationships are unknown.

The Padaukpin limestones are considered by the authors to be Eifelian, thus confirming the work of Cowper Reed (1908). The locality in the valley of the Kelaung chaung is also in limestones, lithologically similar to those of Padaukpin, but the small fauna of corals, brachiopods, and a single species of annelid is a different assemblage. Cowper Reed (1929) regarded the fauna as a whole as indicative of the Givetian. At Wetwin the fossiliferous beds are yellow clay shales, and associated with this change in facies the shales are dominated by lamellibranchs and gastropods but include bryozoa and mud-dwelling brachiopods. The Wetwin Shales represent a local intercalation within the Devonian dolomitic sequence. Cowper Reed (1908: 183) stated that in "view of the absence of stratigraphical and more definite palaeontological indications we may provisionally refer the Wetwin beds to the upper Middle Devonian on the strength of the American affinities". He suggested that these beds overlie the Padaukpin limestones.

In the Zebyngi area La Touche (1913: 166) stated that the Zebyngi beds, then regarded as uppermost Silurian, are succeeded without any apparent stratigraphical break by the basal beds of the overlying dolomite sequence. This seeming paradox is explained by the fact that the Zebyngi beds carry Lower Devonian graptolites. According to Professor W. B. N. Berry, University of California, Berkeley (oral communication, 1967) graptolites from the Zebyngi beds and now in the Sedgwick Museum seem closest to the Bohemian Lower Emsian species *Monograptus atopus*. These are specimens that were labelled *M. dubius* in the Sedgwick collections. Other specimens labelled *M. cf. M. riccartonensis* were determined by Berry as *Monograptus* sp. of the *hercynicus* type.

This paper deals only with the Brachiopoda from the Padaukpin limestones. It is mainly concerned with a revision of the genera and species present in the fauna based on the specimens in La Touche's original collection from the fossiliferous exposure immediately west of Padaukpin village as well as on the specimens in the new collection obtained from this locality and from the previously unknown locality south of the village. The beds at these two places belong to the same horizon and contain an identical fauna so that no distinction is made here between the specimens obtained from one or other of the localities. In addition to describing the species present and considering their systematic position, the age, correlation, and palaeogeography of the brachiopod fauna are also discussed.

La Touche's collection was described by Cowper Reed (1908) who identified forty-five species (excluding three unnamed species of uncertain genus) which he grouped within twenty genera. Of the forty-five species, four were named as new species and four as new varieties by Cowper Reed, and the rest he considered to be species already known from Europe, North America, or China. The authors recognize thirty-two species, including one new species, in the brachiopod fauna from Padaukpin, and as only two of these belong to the same genus thirty-one genera are represented.

The new collection from the Padaukpin limestones is housed in the British Museum (Natural History) and the specimens figured from this collection are catalogued under the code number BB, but there are a few specimens illustrated which came from the La Touche collection in the Sedgwick Museum, and these have a code number beginning with A.

#### II. ACKNOWLEDGEMENTS

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#### III. AGE AND CORRELATION

Reed (1908: 142–146) discussed the age of the fossiliferous beds at Padaukpin that yielded the large fauna he described. He concluded (1908: 143) that the fauna was of late Eifelian age. The correlation is well based because of the relatively high percentage of forms that are either conspecific or closely comparable to those in the Middle Devonian of the Eifel. The brachiopods can certainly be so characterized and the strong representation of the Eifelian coral *Calceola* points to a similar age assignment. Indeed, these broad conclusions based on the overall aspect of the fauna leave little doubt of Middle Devonian age of the containing beds. A significant number of the Padukpin species are not known to occur below the Middle Devonian in the Eifel, but there is always the presumption that a favourable facies

in beds of perhaps late Emsian age would support a fauna of strong Eifelian aspect. However, turning to stocks that are known to cross the Emsian-Eifelian boundary, such as *Reticulariopsis* and *Devonaria*, the strictly post-Lower Devonian position of *R. eifliensis* and *D. minuta* in Europe allows some confidence in a similar age for the beds at Padaukpin.

With regard to the proper assignment of the fauna to the Eifelian or to the Givetian, it must be noted that many of the brachiopods that can be described in the west European nomenclature are species that are known in both the Eifelian and Givetian; notable exceptions are *Devonaria minuta* and *Plectospira ferita*. Neither of these species is known to range above the top of the Eifelian in Europe. However, the strongest indications from the brachiopods of an early Middle Devonian age are afforded by the ribbed spiriferids, *Indospirifer* and *Alatiformia*. So far as the writers are able to discover, both of these have a range of upper Emsian to Eifelian. The external similarity of the new genus and species *Cimicinoides struvei* to the middle Eifelian form called *Cimicinella simulatrix* by Struve (1964) suggests the possibility of an age correspondence based on these forms, especially since *Cimicinoides* has a distinctly different loop structure from the late Emsian-early Eifelian *Cimicinella cimex*.

Part of the Burma sample, weighing 5·4 kg., was processed for conodonts by Dr. G. Klapper of the Pan American Petroleum Corporation, Tulsa, Oklahoma. The following conodonts are listed from the sample:

Polygnathus linguiformis linguiformis Hinde, 1879—(9 specimens)

Polygnathus sp. (cf. Polygnathus xylus sensu Bischoff & Ziegler 1957)—(14 specimens)

indeterminate fragments of Polygnathus Hinde, 1879—(12 specimens)

Angulodus sp. indet. (1 specimen)

Hibbardella sp. indet. (1 specimen)

Hindeodella sp. indet. (1 specimen)

Synprioniodina sp. indet. (1 specimen)

indeterminate fragments of compound conodonts (28)

Belodella triangularis (Stauffer 1940)—(11 specimens)

According to Klapper (written communications, 3rd July, 1966, and 26th May, 1968), the nominate subspecies of *Polygnathus linguiformis* occurs in the Eifelian, Givetian, and in the lowermost part of the *Manticoceras*-Stufe. At least one specimen of the nominate subspecies is also known from the Emsian (Zorgensis-Kalk, Ziegler 1956, pl. 7, figs. 17, 18), although *Polygnathus foveolatus* Philip & Jackson 1967, is the common polygnathid in upper Emsian strata (Schönauer Kalk, Murrindal Limestone, and Taemas Formation). The form listed as *Polygnathus* sp. seems to be closely comparable to specimens assigned to *Polygnathus xylus* in the sense of Bischoff & Ziegler (1957, pl. 5, figs. 11–17). Twelve of the Burma specimens in this category are most like that of Bischoff & Ziegler (1957, pl. 5, fig. 11) from the Kalkige Zwischenschichten (upper Eifelian), whereas the remaining two Burma specimens under this designation are more comparable to that of Bischoff & Ziegler (1957, pl. 5, fig. 13) from the Günteröder Kalk (upper Eifelian). *Polygnathus xylus sensu* Bischoff & Ziegler is reported by them to range from the upper Eifelian into the lower part

of the Givetian (Odershäuser Kalk) and, in the slightly different sense of Bultynck (1966, p. B 199–200, pl. 2, figs. 1–3), is reported to range from the upper Couvinian (Co2d) into the base of the Givetian in Belgium. The remaining conodonts listed do not as yet bear on long-range correlation. Thus the evidence derived from study of the specimens of *Polygnathus*, although admittedly inadequate, would suggest a correlation of the Burma sample with upper Eifelian through lower Givetian strata in central Europe.

It is of interest to note that conodonts have been recorded recently from relatively nearby areas. Conodonts were described from the northern part of west Pakistan (Barnett, Kohut, Rust, & Sweet, 1966). This fauna indicates a Pridoli (i.e. latest Silurian) or Gedinnian (i.e. early Early Devonian) age. The presence of Middle or possibly Upper Devonian conodonts has been noted from near Lutherwan in Kashmir by Gupta, Rhodes, & Austin (1967). These conodont occurrences appear to be older and younger respectively than the Padaukpin occurrence noted here.

#### IV. PADUKPIN FORAMINIFERA

From acid etching of a sample of Padaukpin "limestone" weighing 5·4 kg. a residue of 56·5 gm. was obtained (fraction retained on a 115 microns screen). The residue was "picked clean" over a period of 28 hours, and yielded approximately 1122 identifiable specimens of smaller foraminifers. A few gastropod and smooth-shelled ostracode steinkerns, and a few scolecodont specimens were also obtained. The following foraminifers compose the Padaukpin assemblage:

- A. Agglutinated Form—
  - I. Minammodytes sp. (582 specimens = 51.8%)
  - 2. Hyperammina?-like forms (7 specimens = 0.6%)
  - 3. Hemisphaerammina sp. cf. H. bradyi Loeblich & Tappan 1957, (452 specimens = 40·3%)
  - 4. Metamorphina sp. cf. M. tholsus (Moreman), (27 specimens = 2.4 %)
  - 5. Thurammina?-like forms (34 specimens = 3.0%)
- B. Calcareous Form (pyritized steinkerns)—
  - 6. Nanicella sp. (8 specimens = 0.7%)
- C. Calcareous/or Agglutinated Form (pyritized steinkerns)—
  - 7. Semitextularia sp. cf. S. thomasi Miller & Carmer 1933, (12 specimens = 1.0%).

Paleoecologically, the foraminiferal assemblage is unique in that it is a dominantly encrusting microfauna (over 97%), suggesting that the foraminifers must have lived on some sort of perishable support, i.e., marine grasses. The foraminiferal assemblage is primarily agglutinated, but this is undoubtedly prejudiced by the type of sample preparation (acid residues). Two large (2 inch  $\times$  3 inch) thin-sections were prepared from the limited sample available and searched for calcareous foraminifers, but none were observed. However, the presence in the acid residues of a limited number of pyritized steinkerns of originally calcareous forms such as *Nanicella* and

possibly Semitextularia indicates that originally both agglutinated and calcareous foraminifers composed the microfauna.

Stratigraphically, the foram assemblage appears to be of little help in age-dating the Padaukpin Beds of Burma. This is primarily due to the lack of study of pre-Upper Devonian foraminiferal microfaunas.

It is to be noted that comparable species of agglutinated foraminifers representing the genera *Minammodytes*, *Hyperammina*, *Hemisphaerammina*, *Metamorphina*, and *Thurammina*, are relatively common in rocks as old as Upper Silurian (Wenlockian). Two foraminiferal species from the Padaukpin Beds which may have potential age

Two foraminiferal species from the Padaukpin Beds which may have potential age significance are the foraminifers *Nanicella sp.* and *Semitextularia* sp. cf. *S. thomasi* Miller & Carmer 1933.

The genus Nanicella, up until recently, had been considered as an Upper Devonian form. Mouravieff & Bultynck (1967) however, reported and described pyritized steinkerns, similar to the Padaukpin specimens, from the Couvinian Co2c interval (= Eifelian) of Belgium, in beds which may be roughly of the same age as the Padaukpin Beds of Burma. These two occurrences of Nanicella mark the oldest reported occurrences to date of this genus. Mouravieff & Bultynck (1967) also have illustrated similar pyritized steinkerns from the Frasnian (Upper Devonian) of Belgium. In North America, Nanicella has only been reported from Upper Devonian rocks.

The foraminifer Semitextularia thomasi Miller & Carmer 1933, has been reported (Sobat 1966) from the Middle Devonian (Eifelian) Wissenbacher Schiefer of the Rheinisches Schiefergebirge of West Germany. More recently (Mouravieff & Bultynck 1967) described and illustrated pyritized steinkerns of Semitextularia sp., similar to the specimens from the Padaukpin Beds of Burma, from the Couvinian Colb interval (= Eifelian) of Belgium. Both of these occurrences of Semitextularia, in Burma and Belgium, mark the oldest occurrence of this form to date. In North America, the oldest occurrence of S. thomasi Miller & Carmer 1933, is from the upper Middle Devonian (Givetian) rocks (Wanakah Shale, Hamilton Group) of New York State (Copeland & Kesling 1955). Frasnian pyritized steinkerns of Semitextularia have also been illustrated by Mouravieff & Bultynck (1967).

#### V. PALAEOGEOGRAPHICAL DISTRIBUTION

The brachiopod fauna described in this paper, which may be annotated as the *padaukpinensis* fauna, is recognizable at several localities in southern China or its occurrence is suggested by citation of a few of the diagnostic forms described here.

occurrence is suggested by citation of a few of the diagnostic forms described here.

A faunal occurrence has been noted (China, board of editors and others 1958: 69) from thick beds of dolomitic limestone interbedded with shale and thin bedded limestone in western Yunnan. The reported assemblage consists of Leptaena "rhomboidalis", "Camaroforia" lummatoniensis, Reticulariopsis curvatus, R. aviceps, Sieberella brevirostris, "Atrypa reticularis", Spinatrypa aspera sinensis, Indospirifer padaukpinensis, Aulacella eifeliensis, Productella baitelensis, and Schizophoria striatula. Insofar as comparisons can be made from faunal lists, the western Yunnan occurrence appears to closely duplicate in part the fauna from Padaukpin and may realistically indicate to some extent the paleogeographic distribution of that fauna.

In the French edition of the Chinese Stratigraphic Lexicon (Roger 1965) Indospirifer padaukpinensis is noted in association with Stringocephalus sp., but the accompanying brachiopods, including Spinatrypina bodini (Mansuy), indicate little relation to the padaukpinensis fauna as described here. The cited occurrence is in the Kutaoling Limestone or eastern Kansu Province (Roger 1965: 462–463).

Also in Roger (1965: 653) Indospirifer padaukpinensis is listed in association with Spinatrypina bodini, Atrypa pechiensis, and species of Productella, Emanuella, Schizophoria, Leptostrophia maccarthyi Grabau, and others. This assemblage, from central Hunan, does not include Stringocephalus, but appears to be related to the locality discussed immediately above and not to the padaukpinensis fauna. The presence of Stringocephalus in the latter association supports a Givetian age and certainly Givetian age sedimentary rocks are widespread in China and are represented by Stringocephalus at many localities as noted by Boucot, Johnson & Struve (1966).

In Turkestan, Middle Devonian brachiopod assemblages have long been known that in part resemble the padaukpinensis fauna. Nalivkin (1930, pl. 6, fig. 1) illustrated the rhynchonellid "Hypothyris" pentagona that closely resembles the Burmese specimens. Closest comparisons can be made with the outcrop number 697 in the thick series of silicious and argillaceous shales and limestones composing the Liaglian series in south Ferghana (Nalivkin 1930: 200, 201). Listed brachiopods of locality 697 include "Stropheodonta" subtetragona, "Schuchertella" umbraculum, "Chonetes" minuta, and "Hypothyris" subsignata. Also listed are typical Eifelian species such as "Stropheodonta" lepis and Kayseria lens; also the tetracoral Calceola sandalina. Associated with the typical Eifelian elements (including those that compare closely with the Burmese fauna) are Bohemian-Uralian elements such as Carinatina arimaspus, Janius irbitensis, "Theodossia" superbus, and others. Nalivkin (1930: 218–221) recognized the provincial mixture of brachiopods that compose the Liaglian fauna and reached essentially the same conclusions about provincial relations of the Eifelian faunas as are noted here.

#### VI. EMSIAN FAUNA IN SOUTHEAST ASIA

Amongst brachiopod faunas in close proximity to the area of distribution of the padaukpinensis fauna is the so-called Acrospirifer tonkinensis fauna of northern Indo-China and adjacent regions in the south of China. Principal elements of the tonkinensis fauna, including the nominate species, were first described by Mansuy (1908) with additions in a later paper (Mansuy 1916). An additional valuable study of the tonkinensis fauna was made by Patte (1926). The characteristic brachiopods of the tonkinensis fauna include Acrospirifer tonkinensis, Hipparionyx? lantenoisi, Dicoelostrophia annimitica, Ancylostrophia sp. (= Stropheodonta nov. sp. aff. S. lepis Patte, 1926, pl. 3, figs. 9–13), Machaeraria sp., (= Camarotoechia prolifica Patte, pl. 4, figs. 7–11), and Parachonetes, including P. yenlacensis and probably "Chonetes" zeili (cf. Johnson, 1966: 366). This association appears to be Emsian because of the presence of Acrospirifer tonkinensis, which most closely resembles the lower Emsian guide A. hercyniae. Parachonetes is probably restricted to pre-Eifelian rocks and Ancylostrophia, elsewhere is only known from the Upper Emsian Kondel

Group. Forms like the so-called *Hipparionyx lantenoisi* occur in the Lower Devonian of southeastern Australia.

In southern China the tonkinensis fauna has its best representation in the Yükiang Formation (Wang 1955, 1956) of Kwangsi Province. Wang (1955) recorded Dicoelostrophia as a characteristic element of the Yükiang Formation fauna and in his subsequent paper (1956) he illustrated a probable Parachonetes (Chonetes kwangsiensis Wang 1956, pl. 1, fig. D) and a probable Nadiastrophia or Phragmostrophia (Wang 1956, pl. 3, figs. B, C). Acrospirifer tonkinensis is cited from both Lower and Middle Devonian beds (China, Board of Editors and others 1958: 74, 98, 100, 122), but the listed associated brachiopods are not significant to confirm the identification of the tonkinensis fauna. Similar occurrences are listed by Roger (1965: 426, 562, 564, 612). These are all equivocal faunules, but according to Roger Acrospirifer tonkinensis, Dicoelostrophia annimitica, and a few other brachiopods characterize the Tchanyi beds assigned to the Lower Devonian in central and southern Kweichou Province (Roger 1965: 640).

A number of important elements of the tonkinensis fauna are reported in the Pochiao Shale of eastern Yunnan (Yin 1938) and include Acrospirifer tonkinensis, a probable representative of Ancylostrophia (Stropheodonta inaequistriata var. pattei Yin, pl. 2, fig. 3D) and Dicoelostrophia annimitica. Yin described a dalmanellid from the Pochiao fauna as Thiemella? communis, and this is probably the source of citations of the genus Thiemella in several of the occurrences of the tonkinensis fauna cited above. The form is a peculiar one not easily diagnosed from the published figures, but appears to have some features in common with the dalmanellid genus Reeftonia from the Lower Devonian of New Zealand and southeastern Australia.

#### VII. FAUNAL PROVINCE

The provincial relations of both the *padaukpinensis* and *tonkinensis* faunas appear to be about the same; they consist primarily of genera and species that are characteristic of the Rhenish Community and are particularly lacking in elements that are ordinarily diagnostic of the Bohemian and Uralian subprovinces as defined by Boucot, Johnson, & Talent (1967). In the case of the older *tonkinensis* fauna, one peculiar endemic form, *Dicoelostrophia*, marks the fauna as provincially distinct, but the Eifelian *padaukpinensis* fauna resembles Rhenish Eifelian faunas without any generic exceptions and this points up a certain lessening in provinciality of the Middle Devonian brachiopod faunas compared to those of the Lower Devonian.

Both of the faunas discussed above appear to be restricted geographically and have their principal development between about 15 and 25 degrees north latitude in the southeast Asian peninsula. The Turkestan occurrence is much further north and west, but conveniently located geographically in accordance with its mixed or transitional fauna. The Uralian Lower and Middle Devonian brachiopod faunas are all well to the north even of the transitional Turkestan locality. Rhenish type faunas appear to have undergone a latitudinal shift of some 30 (by comparison with present-day latitudinal positions) degrees in the span of the Eurasian landmass.

#### VIII. SYSTEMATIC DESCRIPTIONS

Phylum Brachiopoda Class ARTICULATA

Order ORTHIDA

Suborder ORTHOIDEA

Superfamily DALMANELLACEA Schuchert 1913

Family RHIPIDOMELLIDAE Schuchert 1913

Subfamily RHIPIDOMELLINAE Schuchert 1913

Genus AULACELLA Schuchert & Cooper 1931

Type species. Orthis eifeliensis Schnur 1853: 213, pl. 37, fig. 6, pro Verneuil 1850: 161 (nom. nud.).

# Aulacella eifeliensis (Schnur 1853)

(Pl. 1, figs. 1-12)

1853 Orthis eifliensis Schnur: 213, pl. 37, figs. 6a-c.

1908 Orthis (Rhipidomella) eifeliensis Reed: 81, pl. 13, figs. 25–26a.

1931 Aulacella eifelensis Schuchert & Cooper: 246.

1932 Aulacella eifelensis Schuchert & Cooper: 122, pl. 19, figs. 7, 8, 10, 11, 13.

1959 Aulacella eifeliensis Biernat: 26, pl. 1, figs. 10-15; pl. 2; pl. 3, figs. 9-10; pl. 12, figs. 1-2.

1965 Aulacella eifeliensis Wright: H333, fig. 212, 1.

MATERIAL. Fifty specimens.

FIGURED SPECIMENS. BB 55500-BB 55507.

Description. Exterior. The valves are subequally biconvex in lateral profile, generally having the pedicle valve strongest posteriorly, and only very slightly convex in its anterior portions. The brachial valve is more evenly curved from front to back. In outline the shells are suboval to subquadrate with a short hinge line and maximum width anterior to midlength. The pedicle valve is more or less flat across its anterior extremities and the brachial valve commonly bears a shallow sulcus that begins at about the dorsal umbo.

The ventral interarea is narrow, less than half the maximum width of the valves, and is nearly flat and triangular and is steeply apsacline to catacline. It is cleft by a triangular open delthyrium. The interarea of the brachial valve is very narrow, flat, triangular, and orthocline.

The external ornament consists of fine radial costellae crossed at irregular intervals by well marked growth lines. The growth lines are uncommon in shells less than I cm. in length, but are prominent anteriorly.

Interior of pedicle valve. The specimens available for description are small and on these the hinge teeth are triangular in their outline parallel to the plane of commissure, but are plate-like on their extremities which are directed toward the anterior portion of the brachial valve. Dental lamellae are not present, but the teeth are supported basally by thickenings of the shell that join the teeth to the wall of the valve. The apex of the delthyrial cavity bears a triangular concave pedicle callist.

The muscle scars are impressed posteriorly and bordered by low bounding ridges around their anterolateral portions. The diductor impressions widen posteriorly, then have subparallel or converging anterolateral edges, and may be faintly flabellate anterolaterally. The adductor scars are not impressed. Generally the anterior half of the diductor impressions is separated by a rounded myophragm.

Interior of brachial valve. The brachiophores in small specimens are triangular and somewhat plate-like, but curved so that the convex surfaces of the plates face dorsomedially. The outer edges of the brachiophores bound the sockets medially and the inner edge of the interarea bounds the sockets posterolaterally. The sockets are developed on the base of the valve which may be slightly thickened and elevated, but no fulcral plates are present. In small specimens the cardinal process arises from the floor of the triangular notothyrial cavity as a rod or prism of suboval cross-section. In larger specimens the cardinal process becomes elongated and erect and wider on its anterior edge, narrowing to a knife-like wedge toward the apex. Larger specimens develop a ponderous myophragm and shell material posteriorly that wholly fills up the notothyrial cavity and increases the size of the brachiophores with pad-like additions of shell material on their medial sides. The myophragm posteriorly is relatively narrow, thick, high, and rounded. It broadens but becomes lower anteriorly. The anterior and posterior adductors are only poorly differentiated by deeper impression of the anterior pair. Muscle bounding ridges are not developed. The posterior adductors are more or less triangular and deeply impressed, especially posteriorly, while the anterior pair is more widely set-apart due to the broad myophragm and each is more or less trapezoidal in outline. The adductor impressions merge almost imperceptibly with the interior of the shell anteriorly.

Internal crenulations. In small pedicle valves the internal crenulations developed

Internal crenulations. In small pedicle valves the internal crenulations developed around the periphery are grouped commonly in two, three, or four with interspaces of various widths separating the individual rod-like elements of the crenulations one from another, and the groups are separated by interspaces that are a little wider than those separating the individuals. In the brachial valve the crenulations also are grouped, but the rods in the several groups are not so well developed, and each group has somewhat flat and grooved appearance rather than a group of rods.

Superfamily ENTELETACEA Waagen 1884
Family SCHIZOPHORIIDAE Schuchert & LeVene 1929
Subfamily SCHIZOPHORIINAE Schuchert & LeVene 1929
Genus SCHIZOPHORIA King 1850

Type species. Conchyliolithus Anomites resupinatus Martin 1809, pl. 49, figs. 13, 14.

## Schizophoria schnuri Struve 1965

(Pl. 1, figs. 13-17)

1908 Orthis (Schizophoria) striatula Reed: 79, pl. 13, figs. 19–24. 1965 Schizophoria schnuri Struve: 202, pl. 19, fig. 4, pl. 20–21.

MATERIAL. Thirty-five specimens.

FIGURED SPECIMENS. BB 55508-BB 55510.

Description. Exterior. The valves are biconvex; in small specimens where the maximum dimension is about a centimeter the valves are evenly biconvex. In larger specimens the relative convexity of the brachial valve becomes greater, becoming very deep and strongly curved throughout its length. Pedicle valves, as they get larger, tend to flatten out anteriorly, so that the place of maximum curvature is well to the posterior, near the umbo. Small specimens are transversely oval in outline, but with short hinge line and maximum width near mid-length. Larger specimens tend to broaden out anteriorly, making the outline subpentagonal with the maximum width anterior to mid-length. Large specimens commonly develop a broad, shallow sulcus in the pedicle valve, but the complementary fold in the brachial valve is only faintly developed.

The exterior bears numerous fine rounded costellae separated by rather narrow interspaces. The costellae increase in number anteriorly both by bifurcation and by implantation. In a few cases newly formed costellae also disappear anteriorly and generally the size of the costellae increases very slightly in width toward the anterior. The costellae are hollow and commonly display small suboval openings at irregular intervals. The costellae are crossed by a few concentric growth lines posteriorly, but the growth lines may become numerous anteriorly on large specimens.

Interior of pedicle valve. The teeth are not well preserved on the available specimens, but appear to be supported basally by shell thickening in the umbonal cavities. Small specimens apparently had dental lamellae that bounded the muscle bounding ridges posterolaterally. Diductor impressions are elongate subpyriform with a variably developed myophragm dividing the impressions medially. Commonly there is some slight flabellation to the anterior edge of the diductor impression which reaches to midlength in larger specimens. The ventral adductor impressions are not discernible. The internal margin is crenulated by the costellae.

Interior of brachial valve. The brachiophores are widely divergent and supported by brachiophore supporting plates that define the sockets on their medial sides. Fulcral plates define the sockets basally. Thickening in and around the brachiophore plates in large specimens causes them to loose their plate-like character. In the notothyrial cavity there is a trilobate cardinal process with a relatively thin triangular plate medially and two smaller rod-like lobes on either side. The adductor muscle scars are poorly impressed forming a nearly subcircular pattern bisected anteriorly by a low myophragm which however is thick and slopes off only gradually laterally. Two pairs of vascular tracks subparallel to the midline emanate from the medial region and continue anteriorly. The internal margin is crenulated by the costellae.

The interarea of the pedicle valve is narrow, commonly less than half the maximum width of the valve and is apsacline, low, triangular, and nearly flat except for the beak which is incurved. The interarea of the brachial valve is well developed, flat, and triangular and is orthocline to hypercline.

#### Family MYSTROPHORIDAE Schuchert & Cooper 1931

DISCUSSION. In the most recent study of the mystrophorids (Cooper 1955),

Kayserella and Mystrophora are contained together in the family Mystrophoridae. Both genera are characterized by relatively well developed elevated dorsal adductor platforms. More recently Wright (1965: H337–339) in his synopsis of the dalmanellid brachiopods has proposed two new families for small septate dalmanellids with dorsal adductor platforms. The writers see no justification for distinguishing Kayserella from Mystrophora at the family level. Very little evidence has been suggested to date to indicate the phylogeny of the small septate dalmanellids which Wright includes in his family Kayserellidae, and therefore the true family associations of the assigned genera are still in doubt. The writers therefore regard Wright's family Kayserellidae as a straight synonym of Schuchert & Cooper's family Mystrophoridae. The subfamily Prokopiinae, which Wright assigns to his family, improperly includes the schizophoriid genus Monelasmina (Cooper 1955: 53; Johnson & Talent 1967). Furthermore we see no reason why Prokopia or Phragmophora should be closely associated with Kayserella.

#### Genus MYSTROPHORA Kayser 1871

Type species. Orthis areola Quenstedt 1871: 589.

#### Mystrophora areola (Quenstedt 1871) (Pl. 1, figs. 18–22)

1871 Orthis areola Quenstedt: 589, pl. 57, fig. 27.

1871 Mystrophora areola Kayser: 612, pl. 13, fig. 5.

1908 Scenidium areola Reed: 82, pl. 13, figs. 28-30.

1955 Mystrophora areola Cooper: 48, pl. 11, figs. 39-50.

MATERIAL. Three specimens.

FIGURED SPECIMEN. BB 55511.

Description. Exterior. The pedicle valves are broadly subpyriform in outline and brachial valves are transversely shield-shaped to suboval. In lateral profile the valves are unequally biconvex with a deep pedicle valve, three or four times as convex as the brachial valve. The convexity of the brachial valve is modified by the presence of a relatively deep sulcus. The ventral beak is prominent and considerably extended posteriorly. The portions of the valve anterior to the umbo are broadly flattened without a median fold, the hinge line is relatively long and straight and equal to slightly more than two-thirds the maximum width which commonly is anterior to midlength. Cardinal angles are obtuse and strongly rounded. The ventral interarea is relatively high and triangular, slightly incurved, and apsacline, although not steeply so. The dorsal interarea is moderately well developed, flat to very slightly incurved, and is anacline. The delthyrium is open and triangular, encompassing an angle of about 30 degrees. There is a small plug of shell material in its apex.

The exterior is covered by numerous low subangular costellae that increase in number anteriorly by intercalation and by bifurcation. Growth lines are not well developed.

#### Genus KAYSERELLA Hall & Clarke 1892

Type species. Orthis lepida Schnur 1853: 218, pl. 45, fig. 9.

#### Kayserella cf. lepida (Schnur 1853) (Pl. 2, figs. 1-3)

1853 Orthis lepida Schnur: 218, pl. 45, fig. 9.

?1908 Kayserella lepida Reed: 77, pl. 13, fig. 15.

1955 Kayserella lepida Cooper: 48, pl. 11, figs. 12-23.

1959 Kayserella lepida Biernat: 36, pl. 3, figs. 1-8.

MATERIAL. Fourteen specimens.

FIGURED SPECIMENS. BB 55512, BB 55513.

DESCRIPTION. Exterior. The shells are transversely shield-shaped in outline and unequally biconvex in lateral profile with the pedicle valve the deepest. The cardinal angles are slightly obtuse and maximum width is commonly near midlength. The ventral interarea is relatively well developed, flat, and triangular and is catacline in its inclination. The dorsal interarea is broad, flat, and also catacline.

The exterior is covered by numerous, fine, subangular to rounded, radial costellae. Concentric ornament is not developed.

Interior structures. No pedicle valve interiors are available. In the brachial valve the cardinal process is triangular and bilobed, crenulated posteriorly. The sockets are set against the posterior valve margin and defined on their inner edges by relatively stout brachiophores. Fulcral plates are not developed, but the shell material may be considerably thickened beneath the bases of the brachiophores and the sockets. There commonly is a more or less well developed notothyrial platform in the apex. A pair of elevated triangular plates originates just above the bases of the brachiophores and projects free anteriorly except along the midline where it joins a blade-like median septum that reaches approximately to the anterior margin of the valve. The median septum also is present dividing the scoop-shaped ventral surface of the adductor platform. Valves are crenulated along the margins by simple, elevated, rounded ridges.

Shell structure. The shell substance is endopunctate.

Order PENTAMERIDA Suborder PENTAMEROIDEA

Superfamily **PENTAMERACEA** M'Coy 1844 Family **GYPIDULIDAE** Schuchert & LeVene 1929 Subfamily **GYPIDULINAE** Schuchert & LeVene 1929

Genus SIEBERELLA Oehlert 1887

Type species. Pentamerus sieberi von Buch in Barrande 1847: 103, pl. 21, figs. 1, 2.

#### Sieberella cf. brevirostris (Phillips 1841) (Pl. 2, figs. 4–12)

1841 Stringocephalus brevirostris Phillips: 80, pl. 32, fig. 143. 1864–65 Pentamerus brevirostris Davidson: 72, pl. 15, figs. 1–14. 1908 Pentamerus (Gypidula) brevirostris Reed: 83, pl. 14, figs. 1–7.

MATERIAL. Fourteen specimens.

FIGURED SPECIMENS. BB 55514, BB 55515.

Description. Exterior. The valves are strongly biconvex with the pedicle valve very deep. The beaks of both valves are strongly incurved with the ventral beak short and directed approximately toward the dorsal umbo. The pedicle valves are roughly pentagonal in outline with width and length approximately equal Brachial valves are transversely subpentagonal. The hinge line is narrow and curved and the cardinal angles are rounded with maximum width at about midlength in medium sized pedicle valves and commonly posterior to midlength in the opposed brachial valves. The pedicle valve bears a broad, low, flat fold that becomes differentiated about half an inch anterior to the ventral beak and the brachial valve bears a broad, shallow sulcus. Shells are plicated anteriorly with the plications beginning about at the point of differentiation of the fold or very slightly posterior in the mid-regions which commonly have three or four plications. The flanks are also plicated, but the plications are of slightly lesser strength and affect the areas adjacent to the fold and sulcus, but not the lateral portions of the flanks.

Interior of pedicle valve. Hinge teeth are not preserved on the available specimens, but beneath the level of the interarea there is a rhomboidal spondylium of deep U-shaped cross-section that is supported by a median septum that continues anteriorly a short distance beyond the edge of the spondylium, sloping off gradually. The umbonal regions on medium and large sized shells are moderately thickened with shell material. The floor of the spondylium is longitudinally grooved by numerous fine striae. Anteriorly, the surface is corrugated by the impress of the plications.

Interior of brachial valve. The inner brachial plates and sockets are not exposed on the available specimens, but the outer plates are very long and closely set together, converging basally to meet where they are supported on a very low ridge-like median septum most of their length. In the prepared internal mould of the brachial valve (pl. 2, figs. 4–7) most of the thickness of the external shell material showed a single plate-like structure but when all the shell material was removed a pair of tracks remained. This apparently is due to deposition of a small amount of shell material over the whole of the interior. The structure must have been closely comparable with that of Sieberella brevirostris as figured by Davidson (1864, 65, pl. 15, fig. 13).

DISCUSSION. The species brevirostris, as originally figured by Phillips, is not a recognizable species and the writers interpret it as illustrated by Davidson as noted in the synonomy above. There are some differences to be noted between the Burmese shells and those illustrated by Davidson. The latter are generally more elongate and have the plications even more poorly developed and on most specimens confined to the fold and sulcus. Burmese shells have fairly well developed plications that are also present on the flanks anteriorly. In shape of the valves and size of the

plications the specimens from Burma more closely resemble a subspecies *Sieberella costata lata* LeMaitre (1952, pl. 16, figs. 22–36), but that species has the plications developed more strongly posteriorly.

# Order STROPHOMENIDA Suborder STROPHOMENOIDEA

Superfamily STROPHOMENACEA King 1846

Family **LEPTAENIDAE** Hall & Clarke 1895

Genus LEPTAENA Dalman 1828

Type species. Leptaena rugosa Dalman 1828: 106, pl. 1, fig. 1.

Leptaena sp.

(Pl. 2, figs. 13, 14)

1908 Leptaena rhomboidalis Reed: 74, pl. 13, fig. 1.

MATERIAL. Six specimens.

FIGURED SPECIMENS. BB 55516, BB 55517.

Description. Exterior. The valves are subsemicircular to subquadrate in outline and planoconvex in lateral profile. Large specimens are dorsally geniculate around the anterior and lateral margins. The hinge line is long and straight and may be the place of maximum width. Some specimens have slightly auriculate cardinal angles. In large specimens there may be a slight widening anteriorly so that the place of maximum width is anterior to midlength. The ventral interarea is long, low, flat, and triangular; its inclination is low apsacline. There is a circular open foramen apically. The triangular delthyrium is mostly closed by an externally convex pseudodeltidium. The interarea of the brachial valve is long, flat, and ribbon-like. Its inclination is low, anacline. There is a well developed, medially cleft, externally convex chilidium closing the notothyrium.

The external ornament consists of concentric rugae crossed by fine rounded radial costellae that are continuous across the crests and troughs of the concentric rugae.

Interior of pedicle valve. The available material does not show the ventral interior to good advantage, however, one exfoliated specimen shows a cordate diductor impression.

Interior of brachial valve. The cardinalia consist of a pair of closely set triangular process lobes that face posteriorly and slightly ventrally, and diverge anterolaterally. The sockets are incised into the shell substance lateral to the cardinal process lobes and are bounded posteriorly by the edge of the interarea. Medially they are bounded by inner socket ridges that are anteriorly continuous with muscle bounding ridges that surround the dorsal adductors. The posterior adductors are broadly spaced and are subtriangular or fan-shaped. They are separated medially by the anterior adductors which are smaller and subpyriform. Both adductor pairs are separated

posteriorly by a low rounded myophragm that narrows anteriorly from the broad base of the cardinal process lobes. At the end of the myophragm and adjoining the anteromedial edges of the anterior adductors, there is a broad, shallow central pit. Anterior to the central pit there is a low triangular breviseptum that is considerably thickened laterally near its highest point. A pair of short brachial ridges is present lateral to the breviseptum and well anterior to the area of adductor muscle attachment. The interior is not crenulated by the external corrugations, but the interior is smooth or is pustulose beyond the areas of muscle attachment. The adductor muscle sites are roughened, evidently formed of different textured shell material than the remainder of the valve.

Shell structure. The shell material is pseudopunctate.

# Superfamily **DAVIDSONIACEA** King 1850 (pro ORTHOTETACEA)

Family UNCERTAIN

Genus XYSTOSTROPHIA Havlíček 1965

Type species. Terebratulites umbraculum Schlotheim 1820.

#### Xystostrophia umbraculum (Schlotheim 1820)

(Pl. 2, figs. 15-20)

1820 Terebratulites umbraculum Schlotheim: 256.

1853 Orthis umbraculum Schnur: 216, pl. 38, fig. 2; pl. 44, fig. 4.

1864,-65 Terebratulites umbraculum Davidson: 76, pl. 16, fig. 6; pl. 18, figs. 1-5.

1908 Orthotetes umbraculum Reed: 75, pl. 13, figs. 2-14.

1966 Schellweinella (Schellweinella) umbraculum Biernat: 59, pls. 9, 10.

1967 Xystostrophia umbraculum Havlíček: 197, pl. 40, figs. 3, 4, 7, 10, 11.

MATERIAL. Eighty-seven specimens.

FIGURED SPECIMENS. BB 55518-BB 55520; Sedgwick Mus. A 2760, A 2762.

DESCRIPTION. Exterior. The valves are sub-semicircular in outline and convexo-concave (resupinate) in lateral profile. The hinge line is long and straight and may be the place of maximum width. Small shells are decidedly transverse in outline, but larger shells gain in relative length with lateral margins commonly at right angles to the hinge line. In these the maximum width may be anywhere between the hinge line and a point in the anterior half of the length of the valves. The anterior commissure is rectimarginate.

The interarea of the pedicle valve is flat, apsacline, and triangular. It bears a broad, triangular delthyrium almost completely covered by the slightly convex pseudodeltidium whose base is arcuate with a concave side facing dorsally.

The interarea is divided into inner and outer parts on either side of the midline. The inner triangular area (secondary area of Thomas 1910) has transverse growth lines that are continuous with those across the pseudodeltidium, and finer grooves perpendicular to the hinge line. Lateral to this, the outer part of the interarea, appears to be unstriated. The interarea of the brachial valve is long and ribbonlike, very low and steeply anacline. The posterior base of the dorsal cardinalia is covered

by a low, almost ribbon-like chilidium that is slightly higher medially on large specimens.

The external ornament consists of numerous radial costellae somewhat elevated and rounded on their crests and separated by broad, U-shaped interspaces. Costellae increase in number anteriorly on both valves by intercalation and individual costellae become slightly wider as they extend anteriorly. The costellae are crossed by a few irregularly and widely spaced growth lines and by very numerous concentric filae that are pominent across the costellae and less well marked in the interspaces. The number of costellae measured in the mid-region of a brachial valve commonly is about 9 in a space of 5 mm., 10 mm. anterior to the beak.

Interior of pedicle valve. The teeth are stubby and triangular and project posteriorly. They are supported basally by long but low dental lamellae that diverge at a high angle, commonly over 100 degrees. The dental lamellae continue as muscle bounding ridges adjacent to transversely oval flabellate diductor impressions posterolaterally. A myophragm is only uncommonly developed crossing from the anterior edge of the adductor impressions to the anterior edge of the diductor impressions. The adductor scars are faintly impressed elongate-suboval. The interior, on most specimens—even the larger ones, is crenulated over most of their surface by the costellae.

Interior of brachial valve. The cardinalia consist of socket ridges that diverge anterolaterally commonly at about 90 degrees to one another. They are connected posteriorly by a flat plate-like structure that serves as the base of a bilobate cardinal process that faces posteriorly. In larger specimens the distal ends of the socket ridges flare laterally in much wider angles, and the anterior edge of the plate bears a short longitudinal ridge medially. The myophore faces on the separate lobes are quadrilobate and approximately parallel to the plane of the ventral interarea. They commonly are visible in the small opening above the pseudodeltidium. The interior is crenulated over most of its area by the impress of the costellae.

Shell structure. The shell material appears to be impunctate and without pseudopunctae.

# Family **STROPHEODONTIDAE** Caster 1939 Subfamily **LEPTOSTROPHIINAE** Caster 1939 Genus *LEPTOSTROPHIA* Hall & Clarke 1892

Type species. Stropheodonta magnifica Hall 1857: 54.

# $\boldsymbol{\textit{Leptostrophia}}\ \mathrm{sp.}$

(Pl. 2, fig. 21; Pl. 3, figs. 1–6)

1908 Stropheodonta (Leptostrophia) palma Reed: 70, pl. 12, fig. 1.

MATERIAL. Three specimens.

FIGURED SPECIMENS. BB 55521-BB 55523.

Description. Exterior. The valves are planate with the brachial valve flat and the pedicle valve having a very faint curvature. The body cavity is very thin. The single articulated specimen is broken so that the outline is uncertain, however,

a few poorly developed growth lines indicate that maximum width probably was slightly anterior to the long straight hinge line and was relatively elongate-subcircular with about equal width and length. The interarea of the pedicle valve is long, flat, and apsacline, more ribbon-like than triangular and it is denticulate the whole of its length. The delthyrium is mostly closed by a convex or subangular pseudodeltidium with a low, open V-shaped space near its base. The interarea of the brachial valve is long, linear, and slightly hypercline.

The external ornament is finely parvicostellate with very closely set costellae.

Interior of pedicle valve. A single fragment of pedicle valve, exposed as an internal mould, reveals a triangular muscle field defined posterolaterally by muscle bounding ridges. It is divided medially by a prominent, narrow myophragm (Pl. 3, fig. 5) For another illustration the reader is referred to the specimen illustrated by Reed (1908, pl. 12, fig. 1) which probably is conspecific.

Interior of brachial valve. The cardinal process lobes are blunt and directed posteroventrally. They are joined on their sides by short socket plates subparallel to the midline that are attached to the cardinal process lobes, but that are considerably shorter. The anterior bases of the socket plates connect with long, strongly divergent ridges that persist about half way to the lateral margins of the valve and diverge slightly from the hinge line. The base of the cardinal process is continuous with a stout, but short, myophragm that narrows and disappears in a short distance anteriorly between the adductor impressions. The adductor scars are not deeply impressed, but are strongly accentuated by the presence of high triangular bounding ridges that adjoin them posterolaterally. Anteriorly they fade imperceptibly into the interior of the shell. The areas lateral to the adductor impressions are pustulose.

## Subfamily LEPTODONTELLINAE Williams 1965

Discussion. Williams (1965: H403) included Leptodontella, Leptodonta, and Parastrophonella in his subfamily. The writers agree that Leptodontella and Parastrophonella belong in close association, but Leptodonta (and the related Altaestrophia) have cardinal process lobes unlike those of Leptodontella or any leptostrophiid, from which the subfamily must have been derived. Leptodonta Khalfin (Williams 1965: H402, fig. 1a) and Altaestrophia Bublitschenko (Khalfin 1948: 255, fig. 33) also lack socket plates like those that characterize Leptodontella and Parastrophonella. Thus we disagree that Altaestrophia Bublitschenko is a junior synonym of Leptodontella Khalfin as it was recorded by Williams (1965: H403). In our conception the subfamily Leptodontellinae comprises Leptodontella, Parastrophonella, Zophostrophia, and Rotundostrophia. All are essentially planate shells, geniculate dorsally or ventrally at a late growth stage. All have leptostrophiid cardinalia with their peculiarly close-set socket plates and all have a relatively similar adductor muscle arrangement and brachial ridge arrangement in the brachial valve.

## Genus *LEPTODONTELLA* Khalfin 1948

Type species. Leptaena caudata Schnur 1853: 224, pl. 42, figs. 4a-c.

#### Leptodontella caudata (Schnur 1853)

(Pl. 3, figs. 7-11)

1853 Leptaena caudata Schnur: 224, pl. 42, figs. 4a-c.

1908 Strophonella caudata Reed: 71, pl. 12, figs. 2–12.

1953 Glossostrophia caudata Williams: 43, pl. 11, figs. 1-4.

1966 Leptodontella caudata Biernat: 50, pl. 7; pl. 8, fig. 17.

1967 Leptodontella caudata Havlíček: 165, pl. 46, figs. 9, 12.

#### MATERIAL. Sixteen specimens.

FIGURED SPECIMENS. BB 55524-BB 55526, Sedgwick Mus. A 2654.

DESCRIPTION. Exterior. In outline the valves are subsemicircular, commonly with acute or even mucronate cardinal angles, giving the outline a transverse shield-shaped aspect. The hinge line is the place of maximum width. In lateral profile the valves are subplanate and the major part of the anterolateral margins on larger specimens are geniculate ventrally. In addition, there is an irregular development of a median U-shaped sulcus in the anterior geniculation where it is reversed and bent toward the brachial valve. The external ornament is not preserved on the available specimens although on those illustrated by Reed there appears to be a faint development of a parvicostellate pattern anteriorly. The interarea of the pedicle valve is long, flat, and low triangular, apsacline in inclination. The apical half of the delthyrium is closed by chevron-like layers of shell forming the pseudodeltidium. The remainder of the delthyrial opening is filled by the cardinal process lobes and socket plates which are covered by a large band-like chilidium. The dorsal interarea is long, ribbon-like, flat, and anacline. Both interareas are denticulate the whole of their length.

Interior of pedicle valve. The ventral process, evident in the material illustrated by Reed, is not well shown on the available material. However, the ventral musculature consists of a very large triangular field moderately impressed and without true bounding ridges. It reaches considerably further anterior than midlength, and generally in large specimens may be semi-flabellate in that its lobes may be divided by short radial ridges near the anterior termination of the scar. The ventral adductor scars are impressed in the posterior part of the muscle field and separated by a broad, rounded myophragm. The diductor scars are smooth, but the remainder of

the interior of the pedicle valve is pustulose.

Interior of brachial valve. The cardinal process lobes are set on thickened shell material posteriorly. They diverge strongly near their bases, then persist subparallel, separated by a relatively broad groove, and face posteriorly. The cardinal process lobes are adjoined laterally by heavy ridge-like socket plates that diverge anteriorly at small angles from the midline. In large specimens the adductor muscle field is relatively broad and the bounding ridges are decidedly elevated and ridge-like. The posterior adductors are widely set kidney-shaped impressions that posterolaterally enclose the closely-set suboval anterior adductors. There is also a well developed set of brachial ridges that emanate from the anterolateral extremities of the posterior adductors and are strongly convex laterally. The area within the brachial ridges may be greatly elevated above the pustulose floor of the valve

anterolaterally, and generally there is a short median ridge continuing anteriorly from the edge of the adductor field. No central pit was noted. Beyond the anterior terminus of the brachial ridges on the one large specimen illustrated there is a broad rounded ridge that continues to the anterior margin of the valve from the raised area enclosed by the brachial ridges. Judging from the specimens of *Leptodontella* that have been seen by the writers the latter is a gerontic feature not seen on most specimens, even of considerable size.

# Subfamily **DOUVILLININAE** Caster 1939 Genus *MESODOUVILLINA* Williams 1950

Type species. Stropheodonta (Brachyprion) subinterstrialis var. seretensis Kozlowski 1929: 96, 97, figs. 28, 29; pl. 4, figs. 1–7.

#### Mesodouvillina birmanica (Reed 1908)

(Pl. 3, figs. 12–17; Pl. 4, figs. 1–4)

1908 Stropheodonta interstrialis (Phillips) var. birmanica Reed : 66, pl. 10, figs. 11–13; pl. 11, figs. 1–6.

MATERIAL. Fifty specimens.

FIGURED SPECIMENS. BB 55527-BB 55531, Sedgwick Mus. A 2738, A 2745.

Description. Exterior. The shells attain medium to large size for the genus and are moderately to strongly concavo-convex. The valves are commonly shield-shaped with the maximum width attained at the hinge line. Well preserved specimens commonly show some development of auricular projections at the cardinal extremities, tending to make the anterolateral margins concave. The convexity of the pedicle valves is modified across the posterior which is nearly flat near the hinge line; but curvature is more even across the transverse dimension anteriorly. From back to front the rate of curvature does not change appreciably so that no real anterior geniculation is developed.

The interarea of the pedicle valve is long, flat, and orthocline, attaining a little greater height near the midline. The interarea of the brachial valve is long, straight, extremely low, and hypercline. The ornament consists of a parvicostellate radial development that coarsens anteriorly due to prominence of the primary costellae. Some specimens have a few well developed concentric growth lines anteriorly.

Interior of pedicle valve. The inner margin of the palintrope is denticulate, commonly along its middle half. The ventral process is a low triangular structure, made prominent by the development of two diverging ridges that make up its lateral edges. Anteriorly it blends with a poorly impressed suboval pair of adductor scars. The diductors are cordate, moderately impressed, but well defined by high, thick, muscle bounding ridges that are nearly straight to gently curved, convex laterally and diverging slightly anteriorly. They are quite widely set apart at their posterior ends. Anteriorly the diductor impressions end abruptly, but without bounding ridges and may be divided medially in their anterior portion by a short but moderately elevated myophragm. The remainder of the interior posteriorly is more or less pustulose, due to the pseudopunctae.

Interior of brachial valve. The posterior margin of the valve is denticulate inside the edge of the interarea. The cardinal process lobes are strongly disjunct, diverging posteriorly with only very slight ventral inclination. The posterior face of each lobe is medially grooved. The socket plates are widely set apart lateral to the cardinal process lobes and are set close to the hinge line, diverging strongly laterally. The adductor impressions are broadly subtrigonal, rounded laterally, and more or less straight, and diverging anteriorly along their medial edges. The lateral portions are bounded by poorly developed, mound-like muscle bounding ridges that diverge anterolaterally. The brace plates originate medially between the adductor impressions and diverge slightly anterolaterally as long, low, pustulose ridges.

# Subfamily **PHOLIDOSTROPHIINAE** Stainbrook 1943 Genus *TELAEOSHALERIA* Williams 1950

Type species. Orthis subtetragona Roemer 1844 (= Shaleria (Telaeoshaleria) sulcata Williams 1950).

# Telaeoshaleria padaukpinensis (Reed 1908)

(Pl. 4, figs. 5-12)

1908 Stropheodonta subtetragona (F. Roemer) var. nov. padaukpinensis Reed: 69, pl. 11, figs. 7–12.

DIAGNOSIS. Posteriorly flat, shield-shaped, sulcate *Telaeoshaleria* with well marked parvicostellate ornament on the pedicle valve.

MATERIAL. Thirty-eight specimens.

FIGURED SPECIMENS. BB 55532-BB 55536.

Description. Exterior. The shells are small to medium sized for the genus. They are subquadrate shield-shaped in outline and plano- to concavo-convex in lateral profile. The hinge line is long and straight and is the place of maximum width. The ventral interarea is well marked; on some specimens faintly triangular near the midline, but for the most part nearly ribbon-like. It is orthocline to gently apsacline and denticulate along the mid two-thirds of its length. The delthyrium is narrow and triangular, enclosing an angle of about 30 degrees. It is completely covered by a flat to very gently convex pseudodeltidium except at its base where a small semi-circular opening is present. There appears to be a complete chilidium. The dorsal interarea is long, linear, and hypercline. The cardinal angles are acute because of the development of small auricular projections. The lateral margins are straight and curve into an anterior margin that is parallel to the hinge line but gently indented. On larger specimens there is a well developed geniculation at about two-thirds of the length and the angle of geniculation is something less than 90 degrees. The geniculate portion of the shell is broadly sulcate medially and the brachial valve is subquadrate and either flat or gently concave.

The exterior bears a well developed parvicostellate ornament with stronger, widely spaced, primary costellae that divide sectors commonly bearing six to twelve very fine radial costellae. The spaces between the primary costellae are flat and may be

corrugated on the posterior portion of the valve, but commonly become concave anteriorly.

Interior of pedicle valve. The diductor tracks are long, narrow, deeply impressed furrows with bounding ridges defining them on their inner and outer sides. There is a V-shaped depression separating them anteriorly. The visceral disc is transversely suboval, well defined, and bounded laterally and anteriorly on larger specimens by a peripheral ridge.

Interior of brachial valve. The cardinal process lobes are medially cleft, but join basally along the midline. Each lobe is strongly furrowed forming a pair of lobes, one facing posteriorly and one laterally. Socket plates are small and ridge-like, situated lateral to the extremities of the cardinal process lobes well to the posterior and strongly divergent anterolaterally. The adductor muscle field is small and transversely subquadrate in outline, defined laterally by strongly elevated, almost plate-like bounding ridges, that are subparallel but converge very slightly anteriorly. The posterior adductors are subtriangular and may be deeply impressed, lying posterolateral in the adductor muscle field. The anterior adductors are also triangular, but are elevated and lie anteromedially within the muscle field. The anterior adductors are joined anteriorly by strong plate-like inner brachial ridges that are faintly arcuate, convex laterally. They are separated at their posterior ends by a faint elliptical central pit. The inner brachial ridge is defined by a more or less elongatesuboval depressed area divided in its anterior portion by a breviseptum of triangular outline and relatively short length. Posterolateral portions of the inner surface are strongly pustulose corresponding to the inner terminations of the pseudopunctae.

COMPARISON. Reed (1908: 69) described the Burma specimens as a variety of Kayser's species *subtetragona*, which they very closely resemble. Specimens of *T. subtetragona* at hand from the Nohner Schichten and the Freilinger Schichten are commonly of larger size, but also are more rounded in the contour of the pedicle valve and appear not to develop concave spaces between the primary costellae.

## Genus RADIOMENA Havlíček 1962

Type species. Orthis irregularis Roemer 1844: 75, pl. 4, figs. 1a-c.

## Radiomena cf. irregularis (Roemer 1844)

(Pl. 4, figs. 13–17)

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1844 Orthis irregularis Roemer: 75, pl. 4, figs. 12-c.
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1962 Radiomena irregularis Havlíček : 471.

1966 Radiomena irregularis Biernat : 58, pl. 8, figs. 14–16.

1967 Radiomena irregularis Harper, Johnson, & Boucot: 431, pl. 9, figs. 6, 7; pl. 10, figs. 1–6.

1967 Radiomena irregularis Havlíček : 131, pl. 25, figs. 1–10.

MATERIAL. Three specimens.

FIGURED SPECIMENS. BB 55537-BB 55539.

DESCRIPTION. Exterior. The pedicle valve is moderately convex, both from the beak to the anterior margin and from side to side. The outline is roughly subquad-

<sup>1853</sup> Leptaena irregularis Schnur: 224, pl. 41, fig. 3.

rate and shield-shaped. The long straight hinge line is slightly less than the maximum width. A few poorly marked growth lines indicate that the cardinal angles are faintly mucronate, with a broadening of the shell anteriorly so that the maximum width is anterior to midlength. No fine ornament is preserved. Shell substance is pseudopunctate.

Interior of brachial valve. There are two fragments of brachial valve in the collections at hand. One is sufficient for description of the cardinalia. The cardinal process lobes are widely set apart ponderous plates with roughly triangular posterior faces. The long axes of the two plates diverge strongly anterolaterally. Their medial faces are concave inward, forming a cup-shaped depression open anteriorly. The second fragment includes what are apparently dendritic dorsal adductor impressions, a low breviseptum raised anteriorly into a mound-like prominence, and a pair of kidney-shaped structures slightly raised around the edges and irregularly depressed toward their centres.

#### Suborder CHONETOIDEA

#### Superfamily CHONETACEA Bronn 1862

#### Family CHONETIDAE Bronn 1862

#### Genus DEVONARIA Biernat 1966

(synonym Plicodevonaria Boucot & Harper, 1968, p. 162)

Type species. Chonetes zeuschneri Sobolev 1909.

# Devonaria minuta (von Buch 1836)

(Pl. 5, figs. 1-12)

- 1836 Orthis minuta Von Buch: 68, ex Goldfuss ms.
- 1871 Chonetes minuta Kayser: 633 (with a synonymy).
- 1908 Chonetes minuta Reed: 78, pl. 13, figs. 16, 17.
- 1962 Retichonetes minutus Muir-Wood: 63, pl. 4, figs. 8–11. 1968 Plicodevonaria minuta Boucot & Harper: 162, pl. 28, figs. 2–10.

MATERIAL. Twenty-two specimens.

FIGURED SPECIMENS. BB 55540-BB 55544.

Description. Exterior. The valves are roughly shield-shaped in outline with a very prominent ventral umbo. Either length or width may be the maximum dimension. In lateral profile the valves are deeply concavo-convex with a very strongly incurved ventral beak. The ventral interarea is anacline, flat, and ribbon-like or slightly incurved near the midline. The delthyrium is low, triangular, and is closed apically by an externally convex crescentic pseudodeltidium. The remainder of the delthyrium is filled by the cardinal process. The interarea of the brachial valve is well defined and flat with a height equal to about one-third to one-half of that of the pedicle valve and with equal length. The dorsal interarea is hypercline.

The exterior is covered by strong, rounded, radial costae separated by well defined U-shaped interspaces that are commonly slightly narrower than adjoining costae.

A few plications bifurcate anteriorly on the pedicle valve and new plications are generally added on the brachial valve by intercalation. On the brachial valves where it is easier to observe the origin of costae only a few are observed that continue from the dorsal beak. Progressively lateral costae originate along the hinge line and the lateralmost costae originate anterior to the hinge line, but so disposed that their posterior projection would intersect the hinge line. Reed's figures (1908, pl. 13) well illustrate a fine concentric ornament of filae across the crests of the costae. The preservation of our material is too poor to well display the fine ornament, but faint vestiges of the concentric filae were observed on one specimen.

Interior of pedicle valve. Hinge teeth were not observed on the available specimens. The hinge line is denticulate, most of its length. The musculature is poorly

impressed and is divided posteriorly by a blade-like median septum.

Interior of brachial valve. The cardinal process is a triangular block with four lobes on its posterior face. Internally it is bilobate and consists of an elongate mound-like region with a faint medial groove. Long, prominent inner socket ridges diverge anterolaterally from the lateral bases of the cardinal process. There is a pair of short divergent anderidia lateral to a long subparallel pair of accessory septa and a breviseptum. The latter structures originate at about midlength of the anderidia adjoining them. In the largest and thickest shelled specimens the anterior ends of the accessory septa are thickened and join laterally with slightly raised, concentrically disposed brachial ridges. The posterior points or origin of the brachial ridges, however, are too faintly developed to ascertain with any certainty. The interior is not crenulated by the impress of the costae.

#### Suborder PRODUCTOIDEA

Superfamily PRODUCTACEA Gray 1840

Family PRODUCTELLIDAE Schuchert and LeVene 1929

Genus PRODUCTELLA Hall 1867

Type species. Productus subaculeatus Murchison 1840: 255.

Productella? sp.

(Pl. 5, figs. 13-17)

MATERIAL. Two specimens.

FIGURED SPECIMEN. BB 55545.

DESCRIPTION. Exterior. The valves are of about equal width and length with the anterior rounded and the posterior modified by the rounded ventral beak protruding posteriorly past a short straight hingeline. In lateral profile the valves are deeply concavo-convex. The ventral beak is short, strongly incurved, and blunt posteriorly. The delthyrium is low and trapezoidal. The ventral interarea is flat and hypercline and equal to just a little more than half the width. The dorsal interarea is linear; no chilidium was noted. The cardinal angles are blunt and rounded

without any indication of auriculation, but the deeply convex ventral umbo is distinct from the posterolateral flanks that flatten out. The areas adjacent to the umbo may be concave; the remainder of the valve anteriorly is strongly convex. The brachial valve is generally concave except for the posterolateral margins that are flatter. The exterior is sparsely covered with irregularly distributed knob-like spine bases that are not set on radial ridges. The anterior portion of one pedicle valve shows the spines preserved. They are long and tube-like and lie flat against the valve in a radial fashion. The concentric ornament consists of very fine irregular lirae.

Interior structures. The available specimens do not expose the interior, but the posterior face of the cardinal process is visible through the open delthyrium. A pair of lobes, diverging ventrally, are exhibited. On the outside of the brachial valve there is a small knob-like "umbo" like that typically developed on specimens that bear an internal alveolus at the anterior edge of the cardinal process. A medial line in the shell material of the brachial valve indicates the presence of a breviseptum.

# Order RHYNCHONELLIDA Suborder RHYNCHONELLOIDEA Superfamily **RHYNCHONELLACEA** Gray 1848 Family **UNCINULIDAE** Rzhonsnitskaya 1956 Genus *UNCINULUS* Bayle 1878

Type species. Hemithyris subwilsoni d'Orbigny 1850 : 92.

#### Uncinulus subsignata (Reed 1908)

(Pl. 5, figs. 18-31; Text-figs. 2, 3)

1908 Rhynchonella (Camarotoechia?) subsignata Reed: 93, pl. 14, figs. 19–22; pl. 15, figs. 1–4. 1930 Hypothyris subsignata Nalivkin: 79, pl. 4, figs. 14, 15.

MATERIAL. Seventy-nine specimens.

FIGURED SPECIMENS. BB 55546-BB 55549, BB 55589A & B.

Description. Exterior. The valves are subtrigonal in outline with long straight posterolateral margins diverging from a beak angle of about 100 degrees or slightly more. The valves are unequally biconvex in lateral profile; the pedicle valve is less convex. It is gently convex posteriorly and flattens out toward mid-length. The brachial valve is strongly convex with the convexity emphasized by the anterior development of a median fold. The pedicle valve has a median sulcus with a long geniculate tongue that is accommodated by the dorsal fold. The anterolateral flanks of the pedicle valve commonly are slightly reflexed. The hinge line is short and curved. The ventral beak is small, pointed, and only moderately incurved. The dorsal beak is strongly incurved and is not visible on the exterior.

The external ornament consists of low, rounded, simple costae which originate anterior to the umbones of both valves. There are commonly 3 to 5 costae in the ventral sulcus and 6 or 7 costae on each flank. Costae flatten out at the commissure and adjoining them the interspaces become knife-like grooves. The junctions of

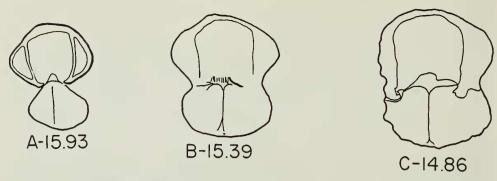


Fig 2. Uncinulus subsignata, serial sections of BB 55589A  $\times$  5·5. Numbers indicate distance in millimeters from the anterior. Original length was 16·18 mm.

adjacent plications project as flaps or platelets that interlock by internal insertion beneath the flattened costae of the opposite valve.

Interior of pedicle valve. Extremely short, thin, dental plates are present. The delthyrial cavity is straight-sided, diverging anterolaterally. The adductor scars are impressed moderately posteriorly and are divided by a thin plate-like myophragm. The ventral diductors are not impressed. All ventral musculature is extremely poorly impressed considering what is known to develop in other species of *Uncinulus*. The shell material is thin and the interior is crenulated by the impress of the costae.

Interior of brachial valve. The brachial valve bears a long blade-like median septum that reaches to about mid-length. It supports a shallow V-shaped septalium

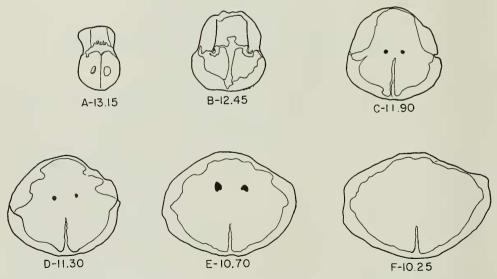


Fig. 3. Uncinulus subsignata, serial sections of BB 55589B × 3. Numbers indicate distance in millimeters from the anterior. Original length was 13.80 mm.

that is covered by a plate of shell material that is longitudinally striate medially forming a comb-like site of diductor attachment. The interior is crenulated anteriorly by the impress of the costae.

#### Genus MARKITOECHIA Havlíček 1959

Type species. Uncinulus marki Havlíček 1956: 568, pl. 9, figs. 5-10, 12.

# Markitoechia? cf. pentagona (Kayser 1871)

(Pl. 6, figs. 1-4; Text-fig. 4)

1871 Rhynchonella parallelpipeda var. pentagona Kayser: 508, pl. 9, fig. 4.

1908 Rhynchonella (Hypothyris) pentagona Reed: 91, pl. 14, fig. 15.

1930 Hypothyris pentagona Nalivkin: 79, pl. 6, fig. 1.

1961 Uncinulus pentagonus pentagonus Havlíček : 147, pl. 27, fig. 8. 1966 Uncinulus pentagonus pentagonus Biernat : 91, pl. 21, figs. 3-15.

MATERIAL. Nine specimens.

FIGURED SPECIMEN. BB 55550, BB 55589C.

DESCRIPTION. Exterior. The valves are small, pentagonal in outline, and subequally biconvex subcuboidal in lateral profile. The ventral beak is short, stubby, slightly incurved, and bears an apical foramen. The beak of the brachial valve is relatively prominent and closely adjoins the ventral palintrope at the edge of the ventral foramen. There is a broad faint sulcus in the pedicle valve anteriorly. The anterior commissure is bowed slightly toward the brachial valve medially, and there is a hump-like fold anteriorly on the brachial valve. There are 7 or 8 low rounded costae on each flank of the pedicle valve and 5 to 7 costae in the sulcus of the pedicle valve. The costae on the flanks are disposed radially, but the lateral costae in the sulcus are added anterior to the umbo and subparallel to the midline of the valves.

At the commissure the costae flatten out and become wider at the expense of the bounding interspaces which become very narrow and groove-like. The points of



A-7.85





Fig. 4. Markitoechia? cf. pentagona, serial sections of BB 55589C  $\times$  10 (section A) and  $\times$  12 (sections B, C). Numbers indicate distance in millimeters from the anterior. Original length was  $8\cdot25$  mm.

juncture of adjoining costae extend as spines accommodated by the flat dorsal costae. This is seen in partially exfoliated specimens as elevated dorsal costae that terminate a slight distance dorsal to the valve margin along the anterior geniculate portion of the valves.

Internal structures. An internal mould of one specimen reveals very short, thin dental lamellae in the pedicle valve and a long thin median septum in the brachial valve. The dorsal cardinalia were not seen.

#### Family YUNNANELLIDAE Rzhonsnitskaya 1959 Genus SCHNURELLA Schmidt 1964

Type species. Terebratula schnurii deVerneuil 1840 : 261.

Schnurella cf. schnuri (deVerneuil 1840)

(Pl. 6, figs. 5, 6)

1840 Terebratula schnurii de Verneuil : 261, pl. 3, fig. 2.

1853 Terebratula schnurii Schnur: 179, pl. 23, fig. 8.

1908 Rhynchonella (Hypothyris) schnuri Reed: 91, pl. 14, figs. 16–18.

1965 Schnurella schnuri Schmidt: 17, fig. 22.

MATERIAL. The single specimen illustrated was the only one available for study. Figured specimen. Sedgwick Mus. A 2779.

Description. Exterior. The specimen is subtrigonal in outline with a poorly developed ventral sulcus and dorsal fold. The exterior is covered with numerous low radial lirae that do not bifurcate anteriorly, but which increase in width toward the anterior of the valves. The anterior and anterolateral margins of the shell are plicate.

# Family **CAMAROTOECHIIDAE** Schuchert & LeVene 1929 Subfamily **SEPTALARIINAE** Havlíček 1960 Genus **SEPTALARIA** Leidhold 1928

Type species. Terebratula ascendens Steininger 1853: 61.

#### Septalaria? sp.

(Pl. 6, figs. 7–11)

1908 Camarophoria cf. ascendens Reed: 87, pl. 14, fig. 12.

MATERIAL. The single illustrated specimen was the only one available for study. Figured specimen. BB 55551.

DESCRIPTION. *Exterior*. The specimen is transversely subrhomboidal in outline and strongly unequally biconvex in lateral profile. The pedicle valve is flattened anteriorly and develops a broad, sulcus that projects dorsally as an extremely long geniculate tongue that is accommodated by a great elevation of the brachial valve anteriorly.

Most of the valve surface is smooth, but the anterolateral margins bear low rounded costae. The ventral tongue also bears costae near the point of geniculation, but at the extremities of the tongue the costae become flattened and grooved medially

while the adjoining inner spaces become narrow and groove-like. It appears that the ventral tongue fits inside the extremities of the dorsal costae.

Order SPIRIFERIDA Suborder ATHYRIDOIDEA

Superfamily **ATHYRIDACEA** M'Coy 1844 Family **ATHYRIDIDAE** M'Coy 1844 Subfamily **ATHYRIDINAE** M'Coy 1844

Genus ATHYRIS M'Coy 1844

Type species. Terebratula concentrica von Buch 1834: 123.

Athyris sp.

(Pl. 7, figs. 1-5; Text-fig. 5)

1908 Athyris concentrica Reed: 110, pl. 16, figs. 18, 19.

MATERIAL. Twenty specimens.

FIGURED SPECIMENS. BB 55559, BB 55589D.

DESCRIPTION. Exterior. In outline the shells are rhomboidal and in lateral profile they are subequally biconvex. The pedicle valve bears a prominent pointed incurved ventral beak and a short, curved hinge line equal to about half the maximum width which is met near midlength. Width and length commonly are approximately equal. The ventral beak is pierced by a large circular foramen joining a broad, low, triangular delthyrium anteriorly. Most of the delthyrium is filled with the beak of the brachial valve.

The pedicle valve bears a broad, shallow sulcus and the brachial valve bears a faintly developed fold which manifests itself in some shells as a faintly subcarinate form. The exterior is covered by numerous lamellose concentric growth lines.







Fig. 5. Athyris sp., serial sections of BB 55589D  $\times$  5 (sections A, B) and  $\times$  6 (section C). Numbers indicate distance in millimeters from the anterior. Original length was 14·70 mm.

Interior structures. The pedicle valve bears short dental lamellae set close to the lateral margins of the interior. The brachial valve bears a flat cardinal plate with a

longitudinal median crest on its dorsal face. There is a dorsal myophragm, but no median septum.

DISCUSSION. There is some resemblance of the indeterminate species at hand to *Athyris concentrica*, but only a few poorly preserved specimens are available. For this reason and because the named species of *Athyris* show a trend for rather marked variability in form, the Burmese specimens are left specifically indeterminate.

## Family **MERISTELLIDAE** Waagen 1883 Subfamily **MERISTINAE** Hall and Clarke 1895

Genus MERISTA Davidson 1851

Type species. Terebratula herculea Barrande 1847: 382.

#### Merista subdidyma (Reed 1908)

(Pl. 6, figs. 12, 13; Text-fig. 6)

1908 Meristella? subdidyma Reed: 116, pl. 16, figs. 25-27.

MATERIAL. Eleven specimens.

FIGURED SPECIMENS. BB 55552, BB 55589E.

Description. Exterior. The valves are subrhomboidal in outline with the posterior pointed and the anterior margin rounded. In lateral profile the valves are subequally biconvex, but generally the pedicle valve is slightly deeper. The ventral beak is moderately incurved with an apical foramen. The lateral palintropes are somewhat flattened. There is a triangular delthyrium closed medially by a deltidial plate. The dorsal umbo is prominent and knob-like. The pedicle valve bears a very shallow medial sulcus that may be slightly accentuated at the anterior commissure which is deflected toward the brachial valve. External ornament is lacking.

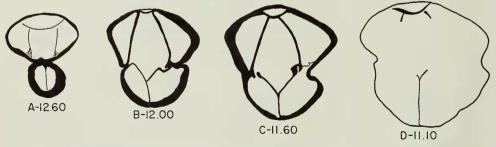


Fig. 6. Merista subdidyma, serial sections of BB 55589E × 5. Numbers indicate distance in millimeters from the anterior. Original length was 13·34 mm.

Interior of pedicle valve. The dental lamellae are long, slender, and plate-like. Their ventral edges rest on the flanks of a long shoe-lifter process that continues anteriorly slightly further than the distal ventral edges of the dental lamellae.

Interior of brachial valve. The dorsal cardinalia consist of a deep V-shaped septalium supported by a long, thin, blade-like median septum.

# Family NUCLEOSPIRIDAE Davidson 1881

Genus NUCLEOSPIRA Hall 1859

Type species. Spirifer ventricosus Hall 1859: 24.

*Nucleospira* sp. (Pl. 6, figs. 14–18)

1908 Nucleospira lens Reed: 111, pl. 16, figs. 21, 21A, 21B; not Schnur 1853.

MATERIAL. Fifty-two specimens.

FIGURED SPECIMEN. BB 55553.

DESCRIPTION. Exterior. The outline varies from sub-circular to sub-oval with either the transverse or longitudinal dimensions being slightly greater. The ventral beak is short, stubby, and strongly incurved over a narrow flat, triangular interarea with length less than half the maximum width of the valves. The interarea is cleft medially by a very broad triangular open delthyrium. The inclination of the ventral interarea is apsacline. The dorsal interarea is not exposed, but apparently is also apsacline. Neither fold nor sulcus are developed.

The exterior is covered with a fine mat of radially arranged thread-like spinules. In the posterior region of the brachial valve the spinules are directed posterolaterally from the dorsal umbo toward the hinge line.

Interior structures. No free specimens are present in the collection, but preparation of an internal mould of one specimen reveals that each valve has a long, low, plate-like median septum extending from the posterior all the way to the anterior margin.

DISCUSSION. The figures of *Nucleospira lens* given by Schnur (1853, pl. 36, figs. 6A–D) are of a subquadrate species, but none of more than a score of specimens from Burma have a subquadrate outline.

#### Suborder RETZIOIDEA

Superfamily RETZIACEA Waagen 1883

Family RETZIIDAE Waagen 1883

Genus PLECTOSPIRA Cooper 1942

Type species. Terebratula ferita von Buch 1834: 96.

#### Plectospira ferita (von Buch 1834)

(Pl. 6, figs. 19-27)

1834 Terebratula ferita von Buch: 76, pl. 2, fig. 37.

1853 Terebratula ferita Schnur: 184, pl. 25, figs. 4a-g.

1960 Plectospira ferita Rzhonsnitskaya: 285, pl. 67, fig. 7.

1966 Plectospira ferita Biernat: 146, pl. 28, fig. 1.

MATERIAL. Thirty-two specimens.

FIGURED SPECIMENS. BB 55554-BB 55556.

DESCRIPTION. Exterior. The outline varies from elongate subpyriform to suboval. In lateral profile the valves are subequally biconvex. The ventral beak is straight and pointed and may be short or of moderate length; it bears an apical foramen. The delthyrium is completely closed with a flat deltidium. The hinge line is very short and rounded and lacks an interarea.

The shells are plicate; each flank of the pedicle valve bears two or three high rounded plications separated by very deep V-shaped to rounded interspaces. Pedicle valves bear a pair of medial plications that tend to bound a sulcus anteriorly. The brachial valve bears a prominent elevated median plication. In the typical form the plications become strongly accentuated anteriorly so that the commissure is sharply deflected into a number of zig-zags. In these specimens generally there is a median rib anteriorly between the pair of median plications on the pedicle valve.

Shell substance. The endopunctate condition is evident under the microscope on almost all of the available specimens.

Discussion. Reed (1908:112) assigned the two specimens that he had available to Kayser's species longirostris and illustrated an elongate subpyriform shell with only moderately developed plications. However, most of the specimens composing the larger group available to the present writers have the typical deep flaring plications of Plectospira ferita. Three of our specimens are, however, in close agreement with Kayser's proposed species and are described below as Plectospira longirostris.

#### Plectospira longirostris (Kayser 1871)

(Pl. 6, figs. 28-32)

1871 Retzia longirostris Kayser: 558, pl. 10, fig. 5. 1908 Ptychospira longirostris Reed: 112, pl. 16, fig. 22.

Material. Three specimens.

Figured specimens. BB 55557, BB 55558.

Description. Exterior. The outline is long-pyriform and the lateral profile is subequally biconvex. The valves are very narrow at the posterior end and this is accentuated by the presence of a relatively long and prominent ventral beak. It bears an apical foramen and a flat, complete deltidium, giving the ventral beak the shape of a truncated cone. The apical angle of the pedicle valve is small and equals about 45 degrees or slightly more. The hinge line is very short and sharply rounded. The anterior margins are evenly curved in a semicircular manner.

The ornament consists of strongly elevated, narrow, radial plications with deep narrow U-shaped interspaces. Pedicle valves commonly have eight plications spaced about equally from one another without the suggestion of a median sulcus. The anterior part of the shell is crossed by relatively prominent concentric growth lamellae that give an imbricate surface to the valves. The anterior commissure is strongly serrate, but lacks the exaggerated zig-zag development of *Plectospira ferita*.

DISCUSSION. This species is distinguished from the more common *P. ferita* in the Burmese collection by the more numerous and narrower plications and by the anteriorly prominent concentric growth lamellae. Furthermore, the ventral beak is relatively longer and more pointed and the hinge line is decidedly narrower in conjunction with a smaller apical angle. Schnur's figures (1853, pl. 25, fig. 4) of

P. ferita show growth lines, but they are not as prominent as those of Plectospira longirostris from the Burmese collection. The accompanying specimens of P. ferita in the latter collection do not appear to have any development of imbricating growth lamellae. The writers considered the possibility that P. longirostris might be a variety or a subspecies of P. ferita, but there seems to be no intergrade between the two forms that are so easily distinguished in the Burmese collection. Therefore we continue to regard them as distinct species.

Suborder ATRYPOIDEA
Superfamily **ATRYPACEA** Gill 1871
Family **ATRYPIDAE** Gill 1871
Subfamily **ATRYPINAE** Gill 1871
Genus **ATRYPA** Dalman 1828

Type species. Anomia reticularis Linnaeus 1758 : 702.

Atrypa "reticularis" (Linnaeus 1758)

(Pl. 7, figs. 6–19)

1908 Atrypa reticularis Reed: 96, pl. 15, figs. 5-7.

MATERIAL. Over 200 specimens.

FIGURED SPECIMENS. BB 55560-BB 55563.

Description. Exterior. Small specimens are lenticular or they may be unequally biconvex with the pedicle valve the deeper. Most small specimens are decidedly elongate suboval with a very short hingeline and maximum width slightly posterior to mid-length. Larger specimens attain a slightly greater relative width with a longer hinge line that modifies the outline to rounded subtrigonal, but with maximum width slightly further posterior and with the length still greater than the width. Medium size specimens with a width of 10 to 15 mm. generally are unequally biconvex with the brachial valves deeper. In large specimens having a width commonly of 25 to 30 mm. or more the brachial valve is deeply convex and the pedicle valve slightly convex to subplanar anteriorly. Outline proportions are roughly the same as for medium size specimens. Beak features for specimens in all size ranges are the same with a very small pointed ventral beak and an apical foramen strongly incurved over the dorsal umbo. No interareas are exposed and no deltidial plates are developed in the pedicle valve. Large specimens commonly develop an anterior geniculate tongue-like sulcus in the pedicle valve with a corresponding strong deflection in the anterior commissure of the brachial valve.

The ornament consists of rounded radial costellae and shallow rounded interspaces or approximately the same width. The density of ribs measured in the midregion of pedicle valves at a distance of 15 mm. anterior to the beak varies slightly, from three to four ribs in a distance of 2 mm. The concentric costae are crossed by imbricating concentric growth lines distributed over the whole of the valves. Frilly growth lamellae are not generally developed except anteriorly on large specimens.

growth lamellae are not generally developed except anteriorly on large specimens.

Interior of pedicle valve. Hinge teeth are stubby and elliptical in cross-section, attached directly to the inner wall of the valve and delineated from the postero-

lateral valve margin by a denticular groove. Short, broadly divergent dental lamellae are present on smaller specimens, but are wholly obsolescent on large ones. The ventral muscle field is large and flabellate, reaching considerably past midlength and commonly is relatively deeply radially striated and raised along its anterolateral edges by a strongly pitted ridge-like thickening of shell material.

Interior of brachial valve. The sockets are broad and shallow with a low corrugated median ridge. Socket plates are discrete, strongly curved posteroventrally, and divergent anteriorly. The notothyrial cavity commonly is built up by a thickening of secondary shell material forming a notothyrial platform. Dorsal musculature is not impressed.

COMPARISON. This form, as developed in the Burmese collections, is closely comparable to the Polish Middle Devonian species *Atrypa subtrigonalis* Biernat (1964, pl. 2).

## Genus *SPINATRYPA* Stainbrook 1951 Subgenus *INVERTRYPA* Struve 1961

Type species. Spinatrypa kelusiana Struve 1956: 385.

S. (Invertrypa) cf. asperoides (Biernat 1964)

(Pl. 7, figs. 20-28)

1964 Spinatrypa asperoides Biernat: 313, pl. 6, figs. 1-5, 12; pl. 7, figs. 7, 8.

MATERIAL. Fifty-one specimens.

FIGURED SPECIMENS. BB 55564-BB 55566.

Description. Exterior. The specimens are small to medium size; commonly the larger specimens attain a maximum width of about 15 mm. In lateral profile the valves are subequally biconvex. Maximum width of most specimens is posterior to midlength. The hinge line is short and rounded, with width and length approximately equal. Most pedicle valves have a slight carination that emphasizes the convexity, but the ventral flanks are also convex. On some of the larger specimens the anterior commissure is slightly bowed toward the brachial valve. The beaks are short, small, and pointed and are incurved over the umbo of the brachial valve. There is a small ventral foramen apically, but no deltidial plates, the area being covered by the posterior edge of the brachial valve.

The ornament consists of rounded radial costae and U-shaped interspaces of the same width, or which may be of slightly less width than the adjoining costae. The latter increase in number anteriorly by bifurcation and by intercalation. At the anterior commissure of specimens between 12 and 15 mm, there are commonly 5 or 6 costae in a space of 5 mm. The radial costae are crossed by evenly spaced frilly growth lamellae, prominent over the whole of both valves.

Interior structures. Interiors are not exposed on the specimens at hand, but one internal mould prepared by removal of the shell shows that dental lamellae are lacking. The ventral diductors appear to be flabellate, but poorly impressed. The costae may be strongly impressed on the internal mould or there may be internal corrugations corresponding to only every 2 or 3 external costae. In the brachial

valve the hinge plates are discrete and widely divergent anterolaterally. Dorsal adductor muscle scars are not impressed.

#### Genus DESQUAMATIA Alekseeva 1959

Type species. D. khavae Alekseeva 1959: 421-424.

## Desquamatia cf. microzonata Struve 1966

(Pl. 8, figs. 1-6)

1908 Atrypa reticularis var. desquamata Reed: 98, pl. 15, figs. 8, 9. 1966 Desquamatia (Synatrypa) microzonata Struve: 151, pl. 16, fig. 12.

MATERIAL. Thirty-three specimens.

FIGURED SPECIMENS. Sedgwick Mus. A 2791, A 2793, A 2794.

DESCRIPTION. Exterior. In outline brachial valves are subcircular with slight variations in width and length so that either may be greater in a group of specimens. The pedicle valve has the aspect of a doubly-truncated circle with the two flat sides diverging posteriorly from a very large apical angle. In lateral profile the shells are more or less lenticular with the pedicle valve commonly slightly deeper in small specimens, but with the brachial valve becoming the deepest in larger ones. hingeline is short and curved. The ventral beak is short, straight, and pointed exposing an apical foramen posterior to conjunct deltidial plates. The beak of the brachial valve is not prominent and is strongly incurved. Most specimens show a slight carination of the pedicle valve in its posterior portion. The brachial valve is evenly rounded. The anterior commissure is rectimarginate.

The external ornament consists of fine, rounded, radial costae separated by Ushaped interspaces about the same amplitude as the joining costae. Costae increase in number anteriorly by splitting, principally on the pedicle valve, and by intercalation, principally on the brachial valve, though exceptions are noted in both cases. Costae are crossed by widely spaced and generally ill-defined concentric growth lines over most of the shell, but which may become slightly lamellose anteriorly on large specimens.

DISCUSSION. The Burmese specimens described above appear to differ slightly from the German Eifelian species (Struve 1966, pl. 16) in having slightly coarser radial costae and slightly better developed concentric growth lamellae at distant intervals. The same comparison may be made with specimens from the Givetian in the Holy Cross Mountains illustrated as Desquamatia prisca by Biernat (1964) pl. 10, figs. 1, 2).

#### Suborder SPIRIFEROIDEA

Superfamily DELTHYRIDACEA Phillips 1841 Family **DELTHYRIDIDAE** Phillips 1841 Subfamily FIMBRISPIRIFERINAE Pitrat 1965

[nom. transl. herein (ex Fimbrispiriferidae Pitrat 1965)]

Genus INDOSPIRIFER Grabau 1931

Type species. Spirifer padaukpinensis Reed 1908: 101, pl. 15, figs. 12-15.

DIAGNOSIS. Biconvex, multiplicate spiriferids, fold and sulcus plicate, fine ornament of radial lirae originating at many points on the valve. Dental lamellae well developed. Excessive shell material lacking posteriorly. Small subdelthyrial plate present. Dorsal cardinalia with crural plates.

Discussion. This genus somewhat resembles a number of Lower Devonian or Eifelian fully ribbed spirifers such as Costispirifer, Fimbrispirifer, and Multispirifer, and a combination of characters serves to distinguish Indospirifer from the others. Indospirifer commonly is easy to distinguish from Costispirifer because of the long outline of the latter, but Costispirifer has low plications with narrow interspaces and without a distinctly developed fold and sulcus in most specimens. The fine ornament of Costispirifer consists of exceedingly fine thread-like radial lirae, very different from the diverging sets of radial lirae of Indospirifer. Multispirifer has coarse angular plications and a well developed subdelthyrial plate in the pedicle valve.

Indospirifer and Fimbrispirifer appear to be closest. They each have a rib pattern in which the sulcus is defined by a pair of primary plications that run all the way from the beak. Lateral plications also emanate from the beak or increase by bifurcation. However, the medial plications in both genera are characterized by a pattern with a median plication and adjoining plications that are subparallel to it (Pl. 8, figs. 9, 14) rather than radial, and which originate along the inner edges of the primary pair that bound the sulcus. Both genera have well developed dental lamellae, although the muscle field in the specimens of Fimbrispirifer studied by the writers is considerably broader than the narrow, elongate muscle field of Indospirifer. In addition, Fimbrispirifer has well developed, finely lamellose, concentric growth lines with concentric rows of fine spines, whereas the fine ornament of Indospirifer is dominated by the subradial pattern with the concentric portion less strongly developed.

Nalivkin (1960: 383, pl. 89, fig. 5) named a species *Indospirifer maritimus* from the Eifelian of Novaya Zemlya. The genus may be widely represented by the so-called *Fimbrispirifer scheii* of the Canadian Arctic (Meyer 1913, pl. 6; McLaren in Fortier *et al.* 1963: 327).

#### Indospirifer padaukpinensis (Reed 1908)

(Pl. 8, figs. 7–15)

1908 Spirifer padaukpinensis Reed: 101, pl. 15, figs. 12–15.

Material. Seventeen specimens.

Figured specimens. BB 55567-BB 55570.

Description. Exterior. The outline of the pedicle valve is rhomboidal and transversely extended. The outline of the brachial valve is subtrigonal to subsemicircular. In lateral profile the valves are strongly biconvex with the pedicle valve the deeper. The ventral beak commonly is prominent and strongly incurved over a well developed moderately long palintrope. Maximum width is at the hinge line or very slightly anterior to it depending on the degree of rounding of the cardinal angles. They may be acute or obtuse, but specimens with mucronate cardinal angles were not observed. The interarea of the pedicle valve is relatively long and only gently curved except near the beak where it is commonly strongly curved.

Its inclination is apsacline, but low, commonly near to the orthocline position. Most of the interarea is deeply striated normal to the hinge line. The material at hand is not sufficient to allow an accurate description of the dorsal interarea. The delthyrium is triangular and open enclosing a relatively broad angle that on large specimens is only a little less than 90 degrees. Flanks and medial regions are both plicate. The flanks bear well developed rounded and elevated plications that commonly are simple, but which may increase in number by branching. The innermost two plications on each flank of the pedicle valve may be a little more greatly elevated than adjoining lateral plications and define the margins of the ventral sulcus. The sulcus is plicate, but the plications commonly are smaller than the adjoining plications on the lateral slopes. The pattern develops around a relatively small median plication on moderate sized specimens. There commonly are two more plications on either side of the median one, but within the sulcus. These additional plications are parallel or nearly parallel to the median plication and they originate from the inner edges of the bounding plications rather than emanating from the ventral beak. On the available specimen that best illustrates the median plications, the fine ornament consists of numerous thread-like raised lirae that may originate from any point on the shell. The lirae diverge out of the interspaces anteriorly and converge over the crests of the plications on the flanks. In the mid-regions they very closely parallel the axes of the median plications.

Interior of pedicle valve. Hinge teeth are plate-like with semicircular dorsal tips whose long axes parallel the interareas. Ventral faces of the hinge teeth are within the delthyrium. The dental lamellae are long, divergent, plate-like, and generally lie just outside the pair of plications bounding the sulcus. The sites of ventral muscle attachment are not impressed although on one specimen there is a short myophragm posteriorly. The apex of the valve is partly closed by a pair of ridges of shell material that are attached to the inner faces of the dental lamellae and which coalesce apically to close a small part of the delthyrium.

Interior of brachial valve. The sockets are poorly preserved on the material available.

Short crural plates are present, and on small specimens project subparallel to the median line, but on larger specimens they converge medially and anteriorly. Generally the area between the crural plates is partly filled with shell material forming a more or less well developed notothyrial platform from which a knob-like site of diductor attachment may arise apically. The site of diductor attachment is deeply striated longitudinally in a comb-like fashion. The dorsal adductors are not impressed, but commonly there is a long thin myophragm. The interior is crenulated by the impress of the plications, but is otherwise smooth.

#### Subfamily **SPINOCYRTIINAE** Ivanova 1959 Genus *ALATIFORMIA* Struve 1963

Type species. Spirifer alatiformis Drevermann 1907: 126; Kayser 1889, pl. 1, figs. 7, 8.

#### Alatiformia? sp.

(Pl. 8, figs. 16-26)

1908 Cyrtina heteroclita var. multiplicata Reed: 108, pl. 16, figs. 11–16, non Davidson.

MATERIAL. Three specimens.

Figured specimens. BB 55571-BB 55573.

Description. Exterior. The outline is subtrigonal and strongly transverse with a long straight hinge line being the place of maximum width. In lateral profile the valves are unequally biconvex with a strong subpyramidal pedicle valve and a very gently convex brachial valve. The pedicle valve bears a well developed U-shaped sulcus equal in width to approximately two and a half of the adjoining plications. The brachial valve develops a low, somewhat flat-topped fold that rises above the adjoining plications and is equal in width to approximately two of the adjoining plications. The ventral interarea is high, flat, and nearly catacline. It is cleft medially by a high triangular open delthyrium enclosing an angle of about 30 degrees. Deltidial plates take the form of rod-like flanges along the inner edge of the delthyrium, but are not plate-like or projecting. The interarea of the brachial valve is not exposed, but evidently is nearly linear and very poorly developed.

The flanks of both valves are radially plicated and each flank of the pedicle valve bears about eight plications emanating from near the beak. There may be three or four more plications that originate away from the beak along the beak ridges. The fine ornament consists of numerous rod-like spine bases arranged more or less in a radial fashion, but not aligned in concentric rows over most of the shell. However, anteriorly where a few poorly developed growth lines occur, there is some differentiation of concentric rows. On the flanks the rods are more or less aligned on radial ridges that diverge out of the interspaces and converge over the tops of the plications. The fold and sulcus lack plications.

Interior of pedicle valve. The hinge teeth are not exposed in the available specimens, but an internal mould of one specimen reveals short, broadly divergent plate-like dental lamellae in the positions of the first interspaces lateral to the ventral sulcus. Medially there is a well defined prominent myophragm, but the ventral musculature is not impressed and is not discernible. The umbonal cavities are wholly free of infilling shell material. Beneath the level of the interarea and in approximately the apical third of the delthyrium, there is a transverse subdelthyrial plate; it is nearly flat and very thin, and may have an internal medial ridge near its dorsal extremity. The ridge is extended dorsally as a medial crest-like projection in the otherwise concave dorsal edge of the plate.

Interior of brachial valve. The available material is not preserved in the region of the cardinalia. The one internal mould available shows the development of a very fine myophragm, but the sites of muscle attachment are not impressed. The interior of both valves is strongly corrugated by the impress of the plications.

## Family **RETICULARIIDAE** Waagen 1883 Genus **RETICULARIOPSIS** Frederiks 1916

Type species. Spirifer (Reticularia) dereimsi Oehlert 1901: 236, pl. 6, figs. 2-16.

#### Reticulariopsis eifliensis (Scupin 1900)

(Pl. 9, figs. 6-20)

1900 Spirifer robustus var. eifliensis Scupin: 56, pl. 5, figs. 5a-d.

1908 Spirifer (Reticularia) aviceps Reed: 105, pl. 16, figs. 1-3, non Kayser.

1908 Spirifer (Reticularia) curvatus Reed: 104, pl. 15, fig. 17, non Schlotheim.

1962 "Spirifer" robustus var. eifliensis Boucot: 416, pl. 51, figs. 12, 13.

1966 Eoreticularia eifliensis Biernat: 126, pl. 30, figs. 13-19.

MATERIAL. Twenty-three specimens.

FIGURED SPECIMENS. BB 55575-BB 55580.

Description. Exterior. Brachial valves are pentagonal in outline and pedicle valves commonly are rhomboidal. Width is characteristically greater than the length on the brachial valves, but the pedicle valves are more nearly equidimensional. The valves are unequally biconvex in lateral profile with the pedicle valve three or four times as deep as the brachial valve. The pedicle valve bears a well defined U-shaped sulcus medially and on some specimens it is accentuated by the development of bordering plications. The brachial valve bears a complimentary fold and on some specimens very faintly developed bounding furrows. The interarea of the pedicle valve is high, triangular, and curved apsacline. The interarea commonly occupies a small portion of the palintrope so that it is considerably less wide than the hinge line and is commonly about half the maximum width of the valves. Beak ridges are well marked, even though they do not coincide with a break in slope of the shell posteriorly.

The delthyrium encompasses an angle of approximately 60 degrees and is bounded laterally by a prominent pair of deltidial plates that meet apically, but which do not close the delthyrium because they are set at angles more nearly normal to the plane of the interarea than parallel to it. The interarea of the brachial valve is narrow, nearly linear, and hypercline. Maximum width is found in the posterior half of the brachial valve and generally near midlength in pedicle valves. The external ornament consists of numerous, evenly spaced, concentric growth lines, each bearing a set of fine radial striae.

Interior of pedicle valve. The teeth are not exposed in the available specimens. Dental lamellae are long, thin plates that diverge anterolaterally at a moderate angle and are set relatively far apart. The sites of diductor muscle attachment are not impressed, but evidently are situated between the dental lamellae and are divided medially by a low rounded myophragm coincident with the internal expression of the ventral sulcus. On some specimens there is a very short, blade-like myophragm 2 or 3 mm. long in the apex on large specimens.

Interior of brachial valve. The sockets are shallow and diverge laterally at wide angles and only slightly away from the hinge line. The median sides of the socket plates are joined by short crural plates that converge basally, but which may either converge or diverge anteriorly. In most specimens a notothyrial platform is developed with a median ridge-like elevation forming the site of diductor attachment. The dorsal adductor impressions are long and narrow and may be bounded laterally by a pair of low bounding ridges.

DISCUSSION. The genus *Reticulariopsis* is now recognized as a senior subjective synonym of *Tingella* following Pitrat (1965: H719).

It appears that there are three recognizable species groups most common in beds of Eifelian age in western and central Europe. The first group, characterized by  $R.\ eifliensis$  and  $R.\ remesi$  (Havlíček 1951: 15, pl. 3, figs. 1, 3), in which the brachial valve is subtrigonal and the pedicle valve is deeply convex with a long palintrope. The second group comprises  $R.\ reticularioides$  (Grabau),  $R.\ dereimsi$  (Oehlert 1901; Vandercammen 1958, pl. 2, figs. 9–14), and  $R.\ bicollina$  (Struve 1961: 332, pl. 1, figs. 1, 2). These last three species are biconvex and transversely suboval in outline with the pedicle valve not so deep and a little more strongly curved in the ventral interarea than the first group. The third group includess species generally assigned to "Spirifer" curvatus Schlotheim (Scupin 1900, pl. 26; see also LeMaitre 1952, pl. 14, figs. 16, 17) which has an extravagant development of ventral sulcus and dorsal fold.

#### Family AMBOCOELIIDAE George 1931 Genus EMANUELLA Grabau 1923

Type species. Nucleospira takwanensis Kayser 1883:86.

#### Emanuella inflata (Schnur 1853)

(Pl. 9, figs. 1–5; Text-fig. 7)

1853 Spirifer inflatus Schnur: 211, pl. 37, figs. 2A-D.

1908 Spirifer (Martinia) inflatus Reed: 106, pl. 16, figs. 5, 5A.

1965 Martinia inflata Jux & Strauch: 58, pls, 1, 2. 1966 Crurithyris inflata Biernat: 122, pl. 29, figs. 1–9.

MATERIAL. Forty-four specimens.

FIGURED SPECIMENS. BB 55574, BB 55589F.

Description. Exterior. The shells are small and unequally biconvex with the pedicle valves larger. Shape is variable; some specimens being transversely subtrigonal to rhomboidal, others are longer than wide and the changes are due to a variable width of the interareas and of the degree of curvature of the ventral beak. The hinge line in all of the specimens is less than the maximum width which commonly is attained posterior to midlength. Cardinal angles are bluntly rounded. The ventral interarea is equal to about one-half to two-thirds the maximum width of the valves; it is triangular and incurved to a variable degree although all inclinations may be described as apsacline. In general, smaller specimens are more steeply apsacline and larger ones may be considerably incurved approaching the orthocline position. Neither fold nor sulcus are developed, although on several specimens a flattening may be seen at the ventral midline anteriorly, suggesting the incipient development of a sulcus there.

The fine exterior ornament revealed, in spite of imperfect preservation, consists of very numerous thread-like radial spinules that may or may not be situated in concentric rows on the growth lines. There appears to be a somewhat greater

tendency to develop a set of spinules along radial lines rather than having each concentric row of spines separately defined as shown in some specimens studied by Veevers (1959: 904). The delthyrium is triangular and open, encompassing an

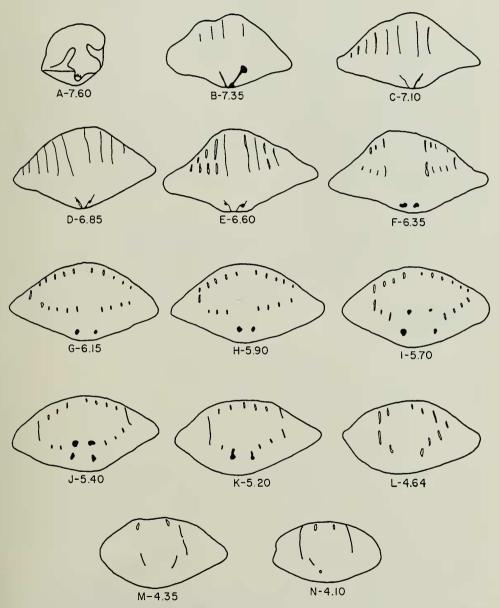


Fig. 7. Emanuella inflata, serial sections of BB  $55589F \times 5$ . Numbers indicate distance in millimeters from the anterior. Original length was 8-60 mm.

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angle of a little less than 30 degrees. The dorsal interarea is short, flat, and triangular and is anacline.

and is anacline.

Interior of pedicle valve. The apex bears a rod-like thickening disposed longitudinally and partly protruding into the apex of the open delthyrium. Hinge teeth develop thick tracks, but are unsupported by dental lamellae.

Interior of brachial valve. The site of diductor attachment in the notothyrial cavity develops comb-like longitudinal striations on a small thickening of shell material apically. Crural plates are present projecting anteriorly and very slightly laterally and converging towards one another at the base of the valve, but the crural plates are not united to form a cruralium supported by a median septum. The crural bases are thick and rod-like in cross section, somewhat more prominent than the thin cural lamellae. They are joined on their ventral edges by a pair of ribbon-like outer hinge plates that continue for some distance anteriorly. The crura continue anteriorly in a subparallel position near the base of the brachial valve and evidently recurve somewhere near the anteromedial portion of the valve to join the primary volutions of the spiralia which consist of 5 or 6 volutions with their apices directed laterally. directed laterally.

#### Superfamily CYRTINACEA Frederiks 1912

[nom. transl. Johnson 1966 (ex Cyrtininae Frederiks 1912)]

# Family CYRTINIDAE Frederiks 1912

Genus CYRTINA Davidson 1858

Type species. Calceola heteroclita Defrance 1828: 306; by subsequent designation of Miller (1889: 342).

#### Cyrtina heteroclita (Defrance 1828)

(Pl. 10, figs. 1-11; Text-fig. 8)

MATERIAL. Sixty-nine specimens.

FIGURED SPECIMENS. BB 55581-BB 55585, BB 55589G.

Description. *Exterior*. The valves are strongly unequally biconvex with a deep subpyramidal pedicle valve and a flat gently convex brachial valve. The ventral interarea is high, triangular, and catacline, commonly flat; but in some specimens the beak may be strongly incurved or incurved and slightly twisted to one side. In outline the valves are subtriangular with a long straight line that is the place of maximum width. The interarea of the brachial valve is relatively long, flat, and

maximum width. The interarea of the brachial valve is relatively long, flat, and orthocline. Most of the specimens are wider than long, with the greatest relative width being about twice that of the length. The ventral beak is pointed and slopes off precipitously toward the anterior and the lateral flanks.

Medially there is a shallow rounded or subangular sulcus without plications. The brachial valve bears a corresponding rounded fold whose elevation appears to be considerably variable. The flanks on both valves are plicate and the number of plications on the flank of a pedicle valve is subject to considerable variability from as few as two, even on large specimens, to as many as seven small plications on other

specimens. The delthyrium is high, triangular, and narrow, commonly encompassing between 10 and 20 degrees. The fine ornament consists of numerous very fine, stubby, rod-like projections aligned on poorly defined radial lirae that diverge anteriorly out of the interspaces and converge over the crests of the plications.

Interior of pedicle valve. The hinge teeth were not observed. There is a pair of long thin dental lamellae paralleling the inner edges of the delthyrium. Dental lamellae converge to meet in the apex of the valve where they join to form a very short median septum. As the dental plates progress anteriorly they join the median septum at continually greater distances above the apex of the pedicle valve and form a spondylium. In the trough between them there is a flatly oval tube-like tichorhinum that is split into a pair of chambers by a blade-like longitudinal process. The median septum continues anteriorly some distance beyond the anterior edges of the convergent dental lamellae. The spiral brachidium consists of a pair of rounded cones. In the specimen sectioned there were five complete volutions in each of the two spiralia and their apices point ventrolaterally at about 45 degrees inclination to the plane of the commissure.

Interior of brachial valve. The sockets are suboval or even subcircular shallow depressions within the interarea. The inner edges of the plates that define the sockets are connected medially by a block of shell material supported by a short pillar-like septum and divided posteriorly into two more or less well differentiated lobes that are longitudinally striate forming a comb-like diductor attachment surface. Outer socket ridges may develop in large specimens. The crura are not preserved. There is a deep depression medially internal to the dorsal fold and the posterior

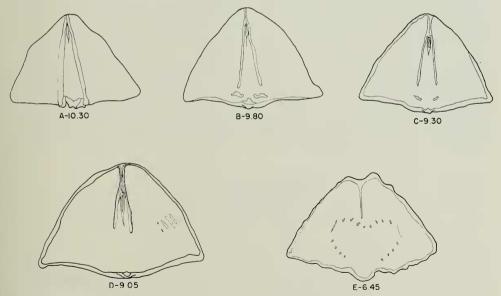


Fig. 8. Cyrtina heteroclita, serial sections of BB 55589G × 2·5 (sections A, B, C) and × 3 (sections D, E). Numbers indicate distance in millimeters from the anterior. Original length was 10·70 mm.

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portion of the shell in this area may bear a slender myophragm, but the adductor muscle impressions are not clearly differentiated.

Shell structure. The shell material is endopunctate. Punctae are densely crowded together without any appreciable pattern.

DISCUSSION. Pitrat in Moore (1965: H678) discarded the subsequent designation of Dall (1877: 24) as invalid and instead selected the subsequent designation of Hall and Clarke (1893: 44). The latter designation was, however, preceded by Miller's noted above.

# Order TEREBRATULIDA Suborder CENTRONELLOIDEA

Superfamily **STRINGOCEPHALACEA** King 1850 Family **MUTATIONELLIDAE** Cloud 1942 Subfamily **CIMICINELLINAE** Stehli 1965 Genus *CIMICINOIDES* gen. nov.

Type species. Cimicinoides struvei sp. nov.

DIAGNOSIS. Externally like *Cimicinella*, but with the loop connected by a horizontal anterior plate which bears a ventrally directed plate-like median septum.

Discussion. This small smooth terebratuloid is a homeomorph of *Cimicinella*. The external configuration is particularly marked in the structure of the ventral beak which bears a delthyrium closed by deltidial plates that are pierced by a hypothyrid foramen. In the presence of short dental lamellae and in the configuration of the cardinalia the two genera are also apparently identical although Stehli (1965: H752) noted that crural plates are present in *Cimicinella*. *Cimicinoides* lacks crural plates and Stehli's indication of their presence in *Cimicinella* evidently refers to the so-called "inneren Troges" shown in Schmidt's reconstruction (1946: 69, fig. 6B, C). The latter is something of an enigmatic structure, unlike anything that the writers are familiar with in Lower and Middle Devonian terebratuloids, but in any event the two individuals of *Cimicinoides struvei* that were sectioned do not show a similar structure.

#### Cimicinoides struvei sp. nov.

(Pl. 10, figs. 12–22; text-figs. 9, 10)

?1908 Glassia whidbornei Reed: 100, pl. 15, fig. 11; not Davidson.

MATERIAL. Thirty specimens.

Figured specimens. BB 55586 (holotype), BB 55587, BB 55588, BB 55589H & I (paratypes).

Description. Exterior. The shells are elongate, subelliptical in outline, and unequally biconvex in lateral profile. Pedicle valves of the larger specimens are

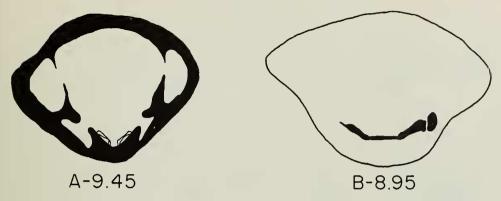


Fig. 9. Cimicinoides struvei, serial sections of BB 55589H × 12. Numbers indicate distance in millimeters from the anterior. Original length was 10.80 mm.

commonly about twice as deep as the brachial valves. The shape is relatively constant with the beak angle about 90 degrees or slightly less, with the posterolateral margins continuing almost straight or they are slightly curved, convex outward. The anterior margin may be evenly rounded from the midline or it may be slightly flattened. The ventral beak is relatively prominent, narrow, and incurved to the suberect position. The ventral palintropes are somewhat flattened and prominent. There is a triangular delthyrium pierced by a hypothyrid foramen. The hinge line is short and rounded. Maximum width is near midlength and the anterior commissure is rectimarginate. The surface of the valves is smooth.

Interior structures. There is a pair of very short thin widely spaced subparallel dental lamellae in the pedicle valve. In the brachial valve the hinge plates are divided posteriorly with their inner surfaces relatively flat and parallel to the surface of the valve. There is a pair of thin layers of shell material forming a faint bilobed notothyrial platform at the apex. Anterior to the sockets the hinge plates join to form a medially flattened cardinal plate. Crural plates are not present. The initial ribbons of the loop are subparallel to the median plane, but twist slightly as they diverge anteriorly so that they are more nearly parallel to the inner surface of the brachial valve. The bands converge again anteriorly a short distance past midlength where they join a small, saddle-shaped median plate that bears a ventrally and posteriorly projecting blade-like median septum. The median plate and median septum bear fine spines of circular cross-section that project anteriorly.

DISCUSSION. Cimincinoides struvei very closely resembles Cimicinella simulatrix Struve (1964, pl. 42) although that species includes slightly larger shells. Struve (1964: 448) described the foramen of C. simulatrix as submesothyrid, a slightly different position than the foramen of C. struvei. Even so these two forms rather closely resemble one another. Further comparison may prove worthwhile when the loop of C. simulatrix is illustrated.

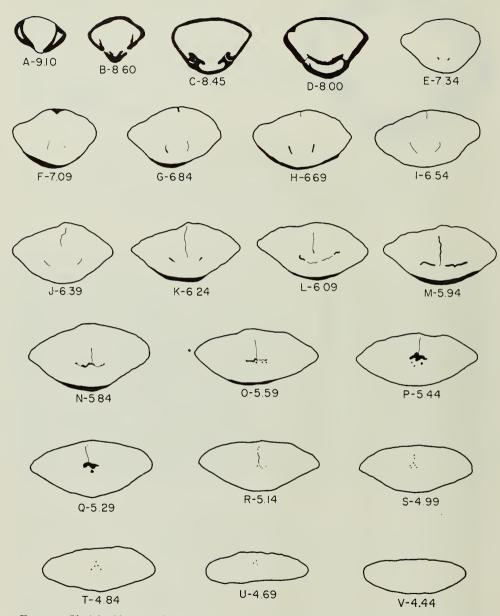


Fig. 10. Cimicinoides struvei, serial sections of BB 55589I  $\times$  5 . Numbers indicate distance in millimeters from the anterior. Original length was 9.45 mm.

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